

# STUDIES IN NEOTROPICAL PALEOBOTANY. IV. THE EOCENE COMMUNITIES OF PANAMA<sup>1</sup>

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## ABSTRACT

The middle(?) to upper Eocene Gatuncillo Formation outcrops near Alcalde Díaz, Panama. From layers of lignite in the formation an assemblage of fossil pollen and spores was recovered, including *Selaginella*, *Ceratopteris*, *Pteris*, monolete fern spores (Types 1–5), trilete fern spores (Types 1–5), cf. *Tillandsia*, Palmae (Types 1–5), cf. *Camptosperma*, *Ilex*, cf. Araliaceae, cf. *Paragonia/Arrabidaea*, cf. *Protium*, cf. *Tetragastris*, *Combretum/Terminalia*, *Casearia*, *Lisianthus*, cf. *Tontalea*, *Alfaroa/Engelhardia* (rare), *Crudia*, Malpighiaceae, cf. *Ficus*, *Eugenia/Myrcia*, *Coccoloba*, *Rhizophora*, *Faramea* and other Rubiaceae, *Cardiospermum*, *Serjania*, *Paullinia*, cf. *Chrysophyllum*, *Pelliceria*, and *Mortoniendron*. Moist lowland communities, as presently occur between the Atlantic side of Gatun Lake and Piña, are well represented, whereas vegetation of higher altitudes and drier habitats is poorly represented or absent. A reconstruction of paleoenvironments, based on varied lines of biological and geological evidence, includes a series of volcanic islands of moderate to low relief, bordered seaward by shallow limestone-depositing coralline communities, and fringed by mangrove swamps of *Rhizophora* and especially *Pelliceria*. Inland communities included tropical moist, tropical wet, and premontane wet forests growing under the general tropical conditions of high rainfall (ca. 2,500 mm) and high uniform temperatures. The lowland insular environment may not record subtle climatic changes more evident in paleocommunities derived from continental areas of greater topographic relief and may reflect paleoenvironmental conditions in the immediate vicinity of the Gatuncillo depositional basin. An assessment of regional paleoclimates and paleogeography must await discovery of other fossil floras, because the Gatuncillo assemblage is the only one of Eocene age known for northern Latin America.

The vegetation characterizing the Eocene epoch in northern Latin America is completely unknown. There has never been a detailed study published on an extensive flora of this age for Central America, Mexico, or the Antilles. Consequently, the Gatuncillo palynoflora of Panama is of interest in providing a first view of this vegetation. The nearest Eocene fossil floras to the south are from the upper Los Cuervos and Mirador Formations of Colombia (Gonzalez Guzman, 1967) and the Rio Turbio Formation of Argentina (Romero, 1977; for a more complete bibliography see Graham, 1973a, 1979a, 1982). The former are of early and middle Eocene age, compared to the late Eocene Gatuncillo palynoflora, and the latter presently treats only the gymnosperms and the Fagaceae. Both belong to a completely different paleogeographic province because at this time South America was isolated between Africa and North America (e.g., Raven & Axelrod, 1974), while the present region of Central America was occupied by a series of volcanic islands trailing south from the North American continent (Coney, 1982; Dengo, 1973).

To the north the closest Eocene floras are from the Mississippi Embayment and Gulf coast region studied by Dilcher and collaborators (e.g., Dilcher, 1973), Elsik (1974), Frederiksen (1980), and others. These are some 2,500 km from the Panama localities. Additional information is provided by Germeraad et al. (1968), Muller (1981), and Graham (1977), but these are either preliminary reports or deal with the fossil record of specific palynomorphs rather than entire palynofloras. The results presented here are considered an initial effort to characterize the Eocene vegetation of central Panama and must be augmented considerably before a detailed concept of the regional paleocommunities, paleoenvironments, and vegetational history can be developed.

## THE COLLECTING LOCALITY

Samples were collected from a roadside exposure of the Gatuncillo Formation near Alcalde Díaz (Peñoncito). The area is shown on the Alcalde Díaz quadrangle map (sheet 4243 II NE,

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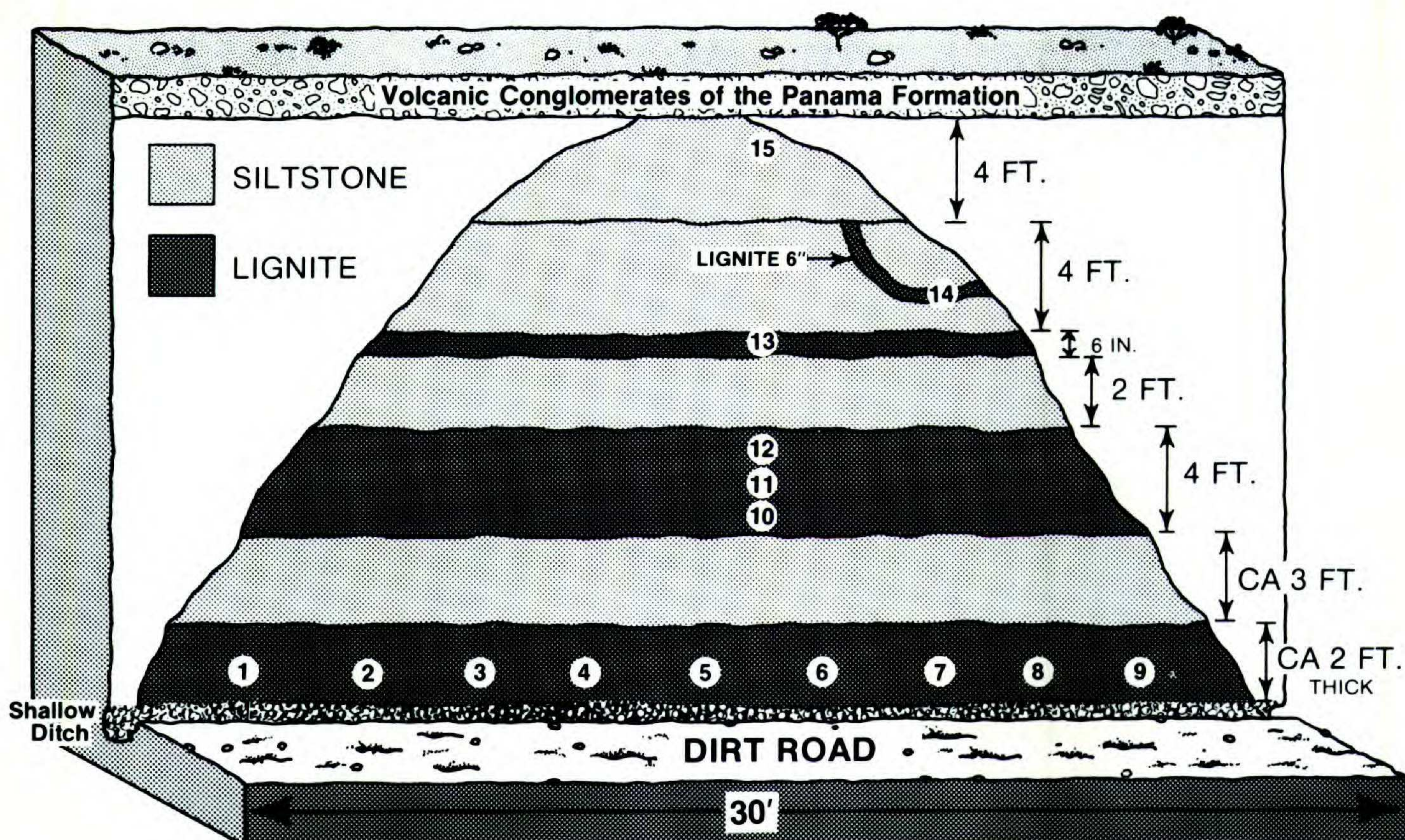


FIGURE 1. Diagrammatic section through roadcut exposure of the Gatuncillo Formation near Alcalde Díaz, Panama (see Graham et al., 1985 for discussion of the locality).

Series E866, scale 1:25,000) prepared by the Army Map Service, Corps of Engineers at coordinates 9°7'N, 79°32'W (North American datum). The site is reached from Panama City by the Boyd-Roosevelt Highway. About 1.8 km from Las Cumbres a dirt road departs to the right. The locality is along this road 2.2 km from the highway intersection.

This site is designated as our locality D and in January 1967, 15 samples were collected (Fig. 1). The beds are tilted at an angle of about 30°. Samples 1–9 are from a basal lignite ca. 0.6 m (2 ft.) thick. This layer is overlain successively by a 0.9 m (3 ft.) siltstone, a second lignite 1.2 m (4 ft.) in thickness (samples 10–12), a 0.6 m (2 ft.) siltstone, a 150 cm (6 in.) lignite (sample 13), a 1.2 m (4 ft.) siltstone with a thin lignite lens (sample 14), and a 1.2 m (4 ft.) siltstone (sample 15) separated from the underlying siltstone by a thin erosion surface. The section is capped by early to late Oligocene conglomerates of the Panama Formation. A visit to the locality in January 1983 revealed that considerable slumping had taken place and the exposure was covered by a nearly uniform veneer of silt 300–460 cm (12–18 in.) thick with a dense overgrowth of herbaceous vegetation (mainly grasses) beginning to develop.

From among the samples, numbers 2, 4, and 9 (all from the lower lignite) yielded the most well-preserved and abundant palynomorphs, and the present study is based primarily on these samples. Slides from the other lignites and the uppermost siltstone were also examined, however, and contained essentially the same microflora. Thus the data base for this study is somewhat limited but not restricted to the microfossils from the lower lignite.

Woodring (1957–1982) has studied the mollusks of the Gatuncillo Formation, and Cole (1952) studied the larger foraminifera. On the basis of the stratigraphic distribution of these fossils in other Caribbean deposits, both authors conclude the Gatuncillo is middle(?) to late Eocene in age. The possibility of a middle Eocene age is considered because three of the larger foraminifera are known elsewhere in strata of this age, and two (*Yaberinella jamaicensis* and *Fabiania cubensis*) are known only from the middle Eocene.

In addition to the lignites and mudstones/siltstones, the Gatuncillo in surrounding areas includes quartz sandstones and coralline and foraminiferal limestones. This lithology reflects deposition in a nearshore coastal environment, and the lignites specifically indicate warm-tem-

TABLE 1. Identification and numerical representation of fossil palynomorphs from the Eocene Gatuncillo Formation, Panama. Figures are percentages based on counts of 200.

	Sample 2	Sample 4	Sample 9		Sample 2	Sample 4	Sample 9
Selaginellaceae				Leguminosae/Caesalpinioideae			
<i>Selaginella</i>	2.5	—	4	<i>Crudia</i>	0.5	3.5	—
Parkiaceae				Malpighiaceae			
<i>Ceratopteris</i>	—	—	15	Type 1	—	—	—
Polypodiaceae				Type 2	—	0.5	2
<i>Pteris</i>	0.5	—	—	Moraceae			
Trilete Fern Spores				cf. <i>Ficus</i>	—	0.5	0.5
Type 1	2	—	—	Myrtaceae			
Type 2	—	—	—	<i>Eugenia/Myrcia</i>	—	0.5	1
Type 3	2.5	0.5	—	Polygonaceae			
Type 4	—	—	—	<i>Coccoloba</i>	—	3.5	2
Type 5	4	1.5	—	Rhizophoraceae			
Monolete Fern Spores				<i>Rhizophora</i>	9	6	10
Type 1	5	1.5	2	Rubiaceae			
Type 2	1	—	1	<i>Faramea</i>	0.5	—	2
Type 3	0.5	—	—	Type 1	—	4	1.5
Type 4	—	—	—	Type 2	—	3.5	1
Type 5	—	—	—	Sapindaceae			
Bromeliaceae				<i>Cardiospermum</i>	—	—	—
cf. <i>Tillandsia</i> Type 1	0.5	1	—	<i>Paullinia</i>	—	0.5	—
cf. <i>Tillandsia</i> Type 2	—	—	—	<i>Serjania</i>	—	—	—
Palmae				Sapotaceae			
Type 1	—	—	—	cf. <i>Chrysophyllum</i>	—	—	2
Type 2	—	2	—	Theaceae			
Type 3	0.5	0.5	—	<i>Pelliceria</i>	0.5	7	11
Type 4	4	2	3	Tiliaceae			
Type 5	3	1.5	1.5	<i>Mortoniendron</i>	1	0.5	—
Anacardiaceae				Unknown Echinete Types			
cf. <i>Camptosperma</i>	—	1	1.5	Type 1	—	—	—
Aquifoliaceae				Type 2	—	—	—
<i>Ilex</i>	—	1	2	Type 3	—	—	—
cf. Araliaceae	—	6	—	Type 4	—	—	—
Bignoniaceae				Type 5	—	—	—
cf. <i>Paragonia/Arrabidaea</i>	—	1	—	Unknown Intectate Type			
Burseraceae				Type 6	0.5	—	0.5
cf. <i>Tetragastris</i>	—	—	—	Unknown Triangular Type			
cf. <i>Protium</i>	—	—	1.5	Type 7	—	—	1.5
Combretaceae				Unknown Oblate/Oblate-Spheroidal Types			
<i>Combretum/Terminalia</i>	—	3	1.5	Type 8	—	—	—
Flacourtiaceae				Type 9	—	—	—
<i>Casearia</i>	—	—	—	Type 10	—	—	0.5
Gentianaceae				Type 11	—	—	—
<i>Lisianthus</i>	0.5	2.5	—	Type 12	2.5	2.5	—
Hippocrateaceae				Type 13	—	—	—
cf. <i>Tontalea</i>	—	—	1	Type 14	—	—	1
Juglandaceae				Type 15	—	—	—
<i>Alfaroa/Engelhardia</i>	—	—	—	Type 16	—	—	—

TABLE 1. Continued.

	Sample 2	Sample 4	Sample 9
Type 17	1	1.5	1
Type 18	2.5	2	—
Type 19	1	—	—
Type 20	—	—	—
Type 21	—	—	—
Unknown Prolate, Tricol(por)ate Types			
Type 22	4.5	5	3.5
Type 23	1.5	—	1
Type 24	3.5	1.5	—
Type 25	—	2	—
Type 26	5.5	3	—
Type 27	3	3	2
Type 28	4	2.5	0.5
Type 29	—	—	—
Type 30	6.5	4	2
Type 31	5.5	0.5	1
Type 32	—	0.5	—
Type 33	—	0.5	—
Type 34	0.5	0.5	—
Type 35	—	2	—
Type 36	2.5	2	—
Type 37	1.5	0.5	—
Type 38	—	—	1
Type 39	—	—	—
Type 40	—	—	—
Other Unknowns	14	11.5	17.5

perate to tropical conditions (Cohen & Spackman, 1972; Scholl, 1964a, 1964b). Other details on the geology of the Gatuncillo Formation are summarized by Graham et al. (1985).

#### MATERIALS AND METHODS

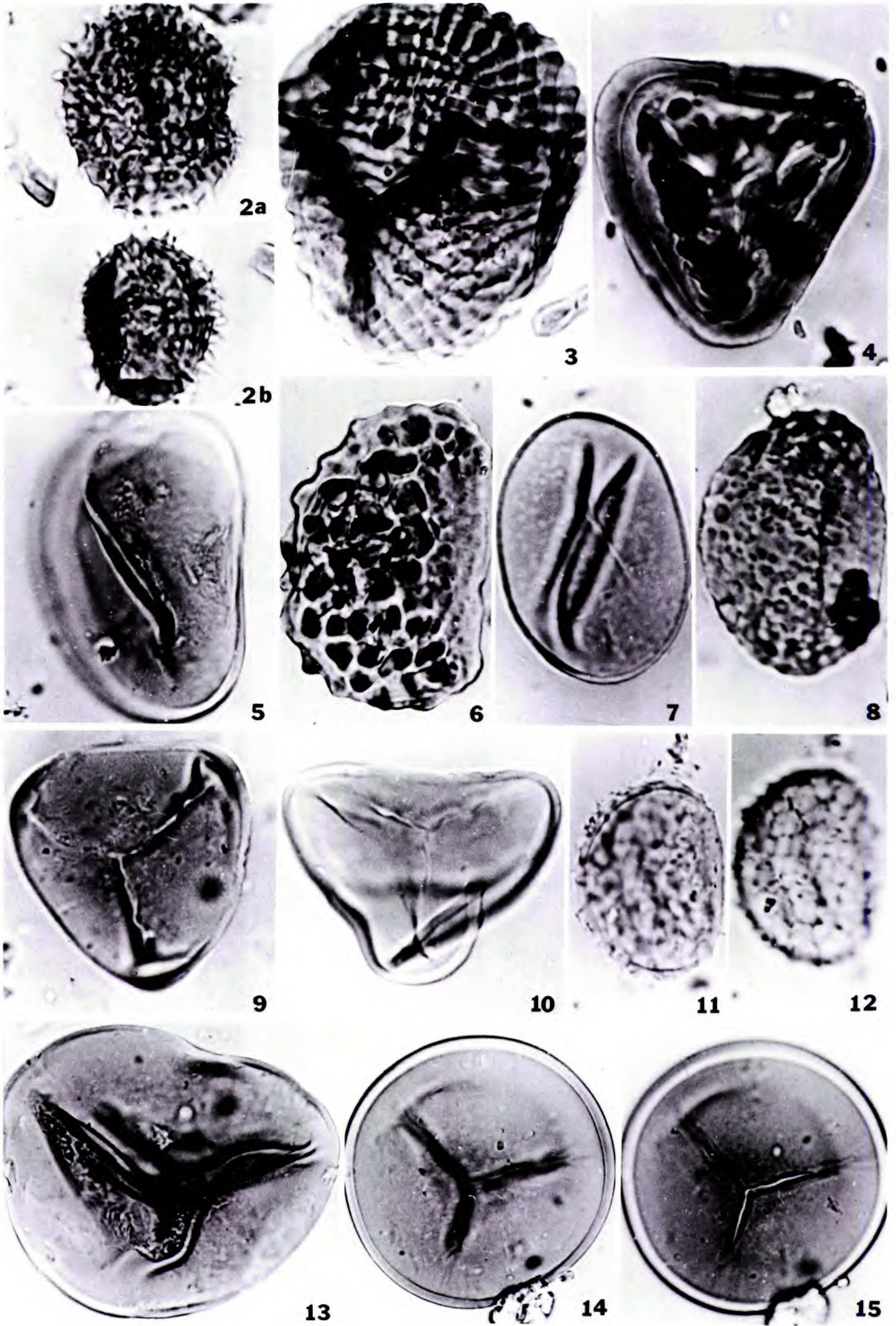
Samples were prepared by cleaning the surfaces to remove contaminants and palynomorphs damaged by oxidation. Pieces of lignite between two and three grams were broken in a mortar and pestle and covered with 10% HCl to remove carbonates. The samples were then passed through HF (to remove silicates), nitric acid (to oxidize lignins and other organic debris), and 10% KOH. Residues were mounted unstained in glycerine jelly and sealed with CoverBond. Photographs were taken with a Zeiss photomicroscope using Panatomic X film. Location of palynomorphs on the slides is indicated by England Slide Finder coordinates. All materials from the study are deposited in the palynology collections at Kent State University.

#### SYSTEMATICS

A total of 47 palynomorphs were identified from the Gatuncillo Formation, and 40 other morphological types were recovered whose biological affinities are unknown (Table 1). The prefix cf. designates the identification is probable, but not as certain as those referred to specific taxa. This is usually due to minor quantitative differences between the modern and fossil pollen or spore that could be the consequence of preservation, or reflect the age difference between the Eocene specimens and their presumed modern analogs. In other instances the specimens may be similar both to a common neotropical genus, and to a taxon from some remote geographic region, characteristic of a completely different biozone (e.g., northern boreal), a rare species, or a plant with exceptionally low pollen production and a highly specific entomophilous pollinating mechanism. Although it may be likely the specimens represent the pollen-prolific, common neotropical genus, it is theoretically possible they represent the other form. The cf. designation is also useful in providing examples of morphologically similar pollen to augment the description and illustration of the fossil specimen (for a more specific example of identification procedures see cf. *Tillandsia* Type 2).

Identification of the microfossils is based on comparisons with taxa in a modern pollen and spore reference collection numbering about 22,000 slides (ca. 20,000 species). To minimize bias in the identifications towards present-day Panamanian or Central American vegetation, our preparations include species from throughout Latin America (Mexico, the Antilles, Central and South America). In addition, exchanges are maintained with some 20 other laboratories throughout the world. Pollen and spore floras, and published results of other paleopalynological studies on Cenozoic deposits in various regions, are also consulted. Consequently, the possibility of bias in the identification of the microfossils towards a given geographic region or a particular community is recognized and is not regarded as a major problem considering the broad coverage of the reference collection and the available literature.

In the pollen descriptions below, sculpture patterns are described as seen under light microscope (LM) magnifications of about 430–970 $\times$ . In some instances a sculpture pattern appearing as faintly scabrate under LM may be revealed as



punctate or microreticulate under electron microscope (EM) magnifications. In such instances the EM pattern can be given in parentheses; e.g., faintly scabrate (EM—microreticulate).

## RESULTS

### SELAGINELLACEAE

*Selaginella* (Fig. 2a, b). Amb ca. circular; trilete, laesurae frequently obscured by wall thickness and sculpture elements, straight, narrow, inner margin entire, ca. 12–15  $\mu\text{m}$  long, extending nearly to spore margin, tapering to acute apex; echinate, echinae short (ca. 2–3  $\mu\text{m}$ ), occasionally curved, base broad, distal face appearing irregularly reticulate due to arrangement of spine bases, proximal face less sculptured; wall 2–3  $\mu\text{m}$  thick (excluding echinae); 25–30  $\mu\text{m}$  and 40–50  $\mu\text{m}$ .

Two size groups of *Selaginella* microspores are present, 25–30  $\mu\text{m}$  (Fig. 2b) and 40–50  $\mu\text{m}$  (Fig. 2a). Both are moderately frequent in samples 2 and 9 (Table 1) and occur scattered throughout the other samples. The genus has previously been reported from Caribbean deposits in the Oligocene of Puerto Rico (Graham & Jarzen, 1969) and in the Miocene of Veracruz, Mexico (Graham, 1976). *Selaginella* is presently distributed widely in tropical regions and is particularly abundant in shaded humid habitats.

### PARKIACEAE

*Ceratopteris* (Fig. 3). Amb oval-triangular, spore margin undulating due to projecting sculpture elements; trilete, laesurae straight, narrow, inner margin entire, 25–30  $\mu\text{m}$  long, extending  $\frac{2}{3}$  distance to spore margin, bordered by narrow (2  $\mu\text{m}$ ) ridged lip, lip surface psilate, margin entire; wall coarsely and conspicuously striate, striae psilate, margin slightly undulating, 2–3  $\mu\text{m}$  wide, prominently developed on distal surface, less distinct approaching laesurae; wall 2–3  $\mu\text{m}$  thick; 55–80  $\mu\text{m}$ .

The genus *Ceratopteris* is a floating aquatic fern distributed from Florida through the An-

tilles and Central America into northern South America. The spores are common in the fossil record under the form-genus name *Cicatricosisporites*. Germeraad et al. (1968) described similar spores as *Magnastriatites*, but Dueñas (1980) considered these congeneric with *Cicatricosisporites*. In the Gatuncillo samples the spores are common in sample 9.

### POLYPODIACEAE

*Pteris* (Fig. 4). Amb triangular, margin entire; trilete, laesurae straight, narrow, inner margin entire, ca. 20  $\mu\text{m}$  long, extending nearly to spore margin; wall with coarse, irregular verrucae on distal surface, proximal surface more laevigate, marginal flange ca. hyaline, 4–5  $\mu\text{m}$  wide; 45–50  $\mu\text{m}$ .

The genus *Pteris* includes about 250 species widely distributed in Latin America. Although some species can occupy dry habitats as primary invaders, most grow in moist areas (in Panama, tropical moist forest; Croat, 1978).

### TRILETE FERN SPORES (FIGS. 9, 10, 13–16)

In addition to *Ceratopteris* and *Pteris*, five other trilete spore types are represented in the Gatuncillo Formation. Although affinities may be suggested for some of these spores, their morphology is too general for definite generic identification.

Type 1 (Fig. 10). Amb triangular; trilete, laesurae slightly undulating, narrow, inner margin entire, 20–25  $\mu\text{m}$  long, extending nearly to spore margin; wall 2  $\mu\text{m}$  thick, laevigate; 35–40  $\mu\text{m}$ .

This spore is similar to several species of *Adiantum*, but lacks diagnostic features separating it consistently from others (e.g., variants in spores of some species of *Dennstaedtia*). It is most common in sample 2 (2%).

Type 2 (Fig. 9). This spore differs from Type 1 in that the wall thickens at the apices and the ends of the laesurae are branched. 45  $\mu\text{m}$ .

Type 3 (Fig. 13). The distinctive feature of this spore is its large size (120  $\mu\text{m}$ ), nearly double

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FIGURES 2–15. 2a. *Selaginella*, 2-1, V-27,1-3.—2b. *Selaginella*, 2-1, Q-31,2.—3. *Ceratopteris*, 9-1, S-36.—4. *Pteris*, 2-1, Q-39.—5. Monolete fern spore type 1, 4-1, O-22,2.—6. Monolete fern spore type 2, 2-1, G-39,2.—7. Monolete fern spore type 3, 4-1, T-7.—8. Monolete fern spore type 4, 2-1, T-32,1-3.—9. Trilete fern spore type 2, 4-1, R-10,4.—10. Trilete fern spore type 1, 4-1, X-8.—11, 12. Monolete fern spore type 5, 4-1, W-12,4.—13. Trilete fern spore type 3, 4-1, N-26,3-4.—14, 15. Trilete fern spore type 4, 4-1, M-38,1-2. (Numbers following plant names indicate the sample and slide number, and England Slide Finder coordinates. All material is labeled locality Pan D, = Gatuncillo Formation from the site described in the text.)



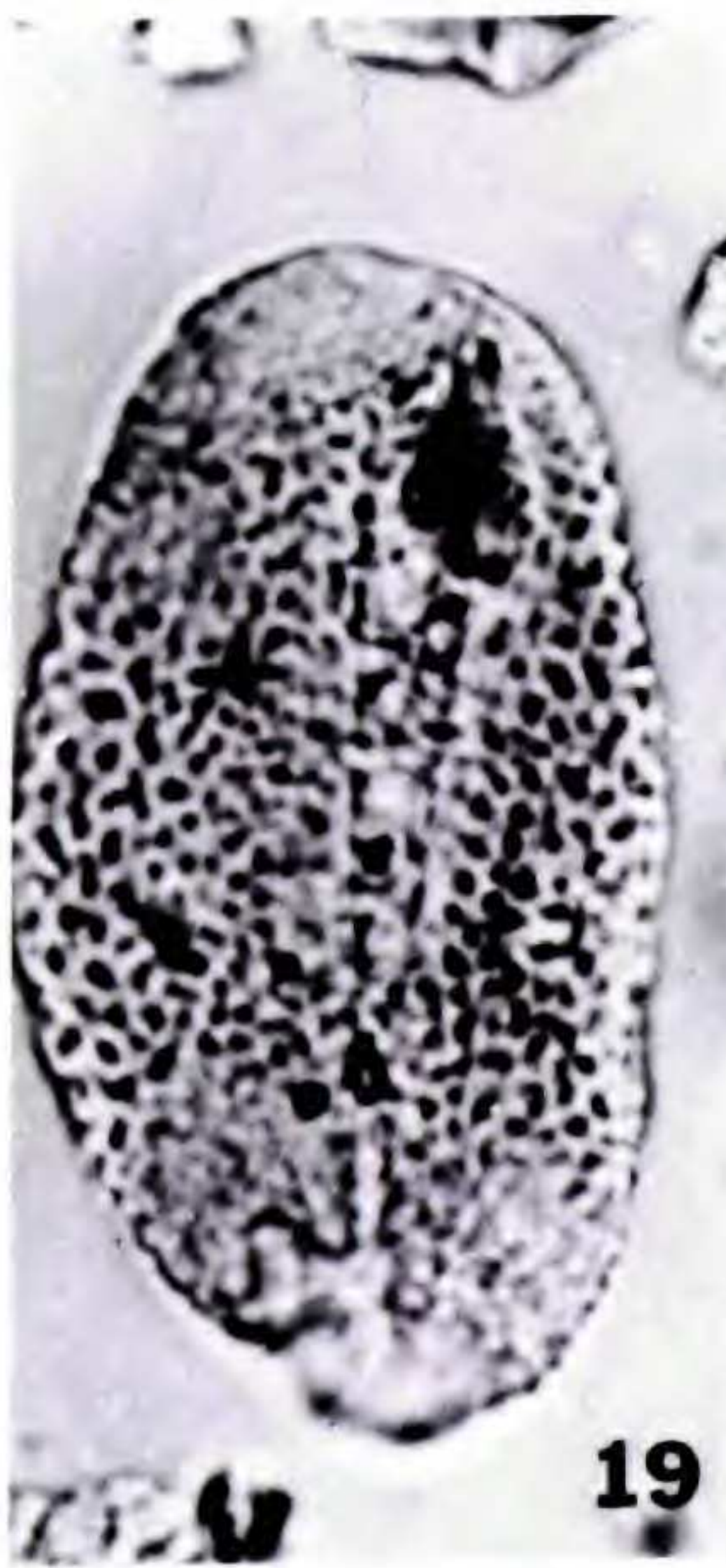
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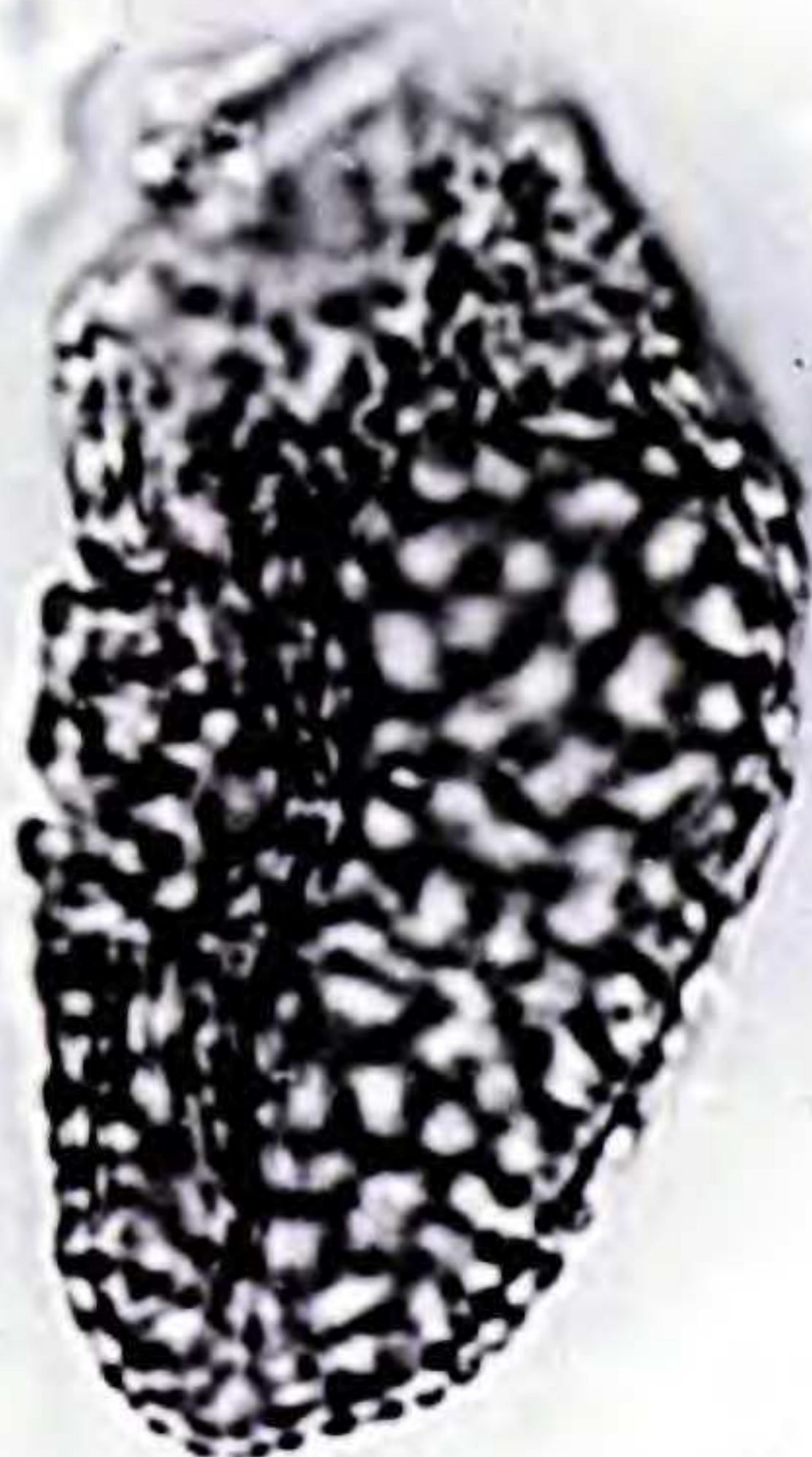
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that of the similar Type 5 (55–65  $\mu\text{m}$ ; Fig. 16). It is most common in sample 2 (2.5%).

Type 4 (Figs. 14, 15). Amb circular; trilete, laesurae straight, narrow, 27–30  $\mu\text{m}$  long, extending  $\frac{1}{2}$ – $\frac{2}{3}$  distance to spore margin, bordered by narrow, ridged lip; wall hyaline, 3–4  $\mu\text{m}$  thick, laevigate, minute pits surrounding laesurae, concentrated in central contact region; 90–100  $\mu\text{m}$ .

Type 5 (Fig. 16). This spore is similar to Type 3 except it is about half the size (55–65  $\mu\text{m}$ ). Similar spores are known in older sediments as *Deltoidospora* and have been reported recently from the Eocene of the Burgos Basin (north-eastern Mexico; Martinez-Hernandez et al., 1980). Among spores in our reference collection it is similar to *Antrophytum* (Polypodiaceae). It is common in samples 2 (4%) and 4 (1.5%).

#### MONOLETE FERN SPORES (FIGS. 5–8, 11, 12)

Monolete fern spores usually cannot be identified to genus within the Polypodiaceae/Blechnaceae complexes. This is especially true of fossil spores that lack the enclosing perine. In the Gattucillo material, two distinct monolete fern spores are common, and three others are present that may represent only variants or preservation forms.

Type 1 (Fig. 5). Amb reniform, outer margin entire; monolete, laesura along concave side, straight, narrow, 20–25  $\mu\text{m}$  long, extending ca.  $\frac{1}{3}$  spore length; wall 2  $\mu\text{m}$  thick, laevigate; 70–75  $\mu\text{m}$  by 45–50  $\mu\text{m}$ .

This spore belongs to the form-genus *Lavigatosporites*, which is a highly artificial taxon and, consequently, has an extensive stratigraphic range (Paleozoic to Recent).

Type 2 (Fig. 6). Amb reniform, outer margin lobate reflecting sculpture elements; laesura straight, narrow, inner margin entire, 30–35  $\mu\text{m}$  long, extending  $\frac{2}{3}$  spore length; wall 3–4  $\mu\text{m}$  thick, verrucate, verrucae prominent on distal surface, diminishing about laesura; 55–65  $\mu\text{m}$  by 35–45  $\mu\text{m}$ .

This spore type belongs to the form-genus *Verrucatosporites* which ranges from the Paleozoic to Recent.

Type 3 (Fig. 7). This spore is similar to Type 1 but has minute punctations over the entire surface. 45  $\mu\text{m}$  by 35  $\mu\text{m}$ .

Type 4 (Fig. 8). This spore is coarsely and irregularly punctate (corrosion artifact?). 50  $\mu\text{m}$  by 35  $\mu\text{m}$ .

Type 5 (Figs. 11, 12). This spore has echinae-like structures with the bases arranged to give a reticulate appearance. It is possible that this apparent sculpture represents remnants of a perine appressed to the spore surface. 50  $\mu\text{m}$  by 35  $\mu\text{m}$ .

#### BROMELIACEAE (FIGS. 17–21)

cf. *Tillandsia* Type 1 (Figs. 17–19). Prolate; monocolpate, colpus straight, narrow, inner margin entire, 45  $\mu\text{m}$  long, extending nearly entire length of grain; tectate-perforate, wall thin (ca. 1.5–2  $\mu\text{m}$ ), reticulate, reticulum fine, lumen slightly irregular in outline, ca. 1–1.5  $\mu\text{m}$  on distal surface, diminishing toward colpus and especially toward poles, muri ca. 1–1.5  $\mu\text{m}$  wide, smooth, margins entire; 50–55  $\mu\text{m}$  by 25–30  $\mu\text{m}$ .

cf. *Tillandsia* Type 2 (Figs. 20, 21). Pollen of *Tillandsia* Type 2 differs from the preceding in having a much coarser reticulum. The diameter of the largest lumen is 3–4  $\mu\text{m}$  (versus 1.5–2  $\mu\text{m}$ ). In other features the grains are similar.

The assignment of these grains to the Bromeliaceae is based on similarity to several species of *Tillandsia*. The specimen illustrated in Figure 19, for example, is especially similar to some grains of *T. excelsa* Griesb. (*Ocampo 001159*, Costa Rica, CR). Other fossil specimens are comparable in morphology but differ slightly in minor, quantitative features (e.g., almost immeasurable, minute differences in diameter of the lumen, wall thickness, height and/or width of the columellae, etc.). These differences are difficult to record accurately and consistently, but they do impart a different aspect to the grains that can be discerned visually. Consequently, the specimens are assigned to the next higher taxonomic rank (family Bromeliaceae), then compared (cf.) to the genus *Tillandsia*.

The fossil record suggests that the middle and

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FIGURES 16–31. 16. Trilete fern spore type 5, 2-1, J-24,4.—17, 18. cf. *Tillandsia* type 1, 4-1, W-30,2-4.—19. cf. *Tillandsia* type 1, 2-1, T-28.—20, 21. cf. *Tillandsia* type 2, 4-1, M-30,2-4.—22. Palmae type 3, 4-1, H-28,4.—23. Palmae type 1, 2-1, V-19,1-2.—24, 25. Palmae type 2, 4-1, V-20,4.—26. Palmae type 4, 2-1, D-16,2.—27. Palmae type 5, 2-1, L-22,1-3.—28, 29. cf. *Camptosperma*, 4-1, Q-25,3.—30, 31. cf. Araliaceae, 4-1, S-14.



late Eocene includes the time interval during which many angiosperms were differentiating into modern genera. In slightly older deposits (e.g., Paleocene, early Eocene) many, perhaps most, angiosperm pollen types cannot be assigned to modern genera. In slightly younger deposits (e.g., Oligocene) most do resemble modern genera. The upper Eocene is intermediate and the Gatuncillo Formation is part of this transition period.

The concepts and procedures illustrated by the identification of the Bromeliaceae cf. *Tillandsia* specimens are considered a conservative approach that minimizes misidentifications while providing the maximum taxonomic and biogeographic information that can reliably be derived from this difficult tropical Eocene material.

#### PALMAE (FIGS. 22–27)

Five morphological categories of palm pollen were recovered from the Gatuncillo Formation. The moderate diversity and sustained numerical representation suggest that palms were a significant, but not a dominant, element in the upper Eocene landscape of Panama (7.5% in sample 2; 6% in sample 4; 4.5% in sample 9; Table 1).

Type 1 (Fig. 23). Oblate, amb triangular to slightly oval triangular with rounded apices; trichotomocolpate, arms straight to slightly sinuous, 18  $\mu\text{m}$  long, narrow, tapering to acute apex, inner margin entire to faintly dentate, extending within ca. 2–4  $\mu\text{m}$  of outer margin; tectate, wall 1.5–2  $\mu\text{m}$  thick, slightly thicker at apices; microechinate, echinae minute, blunt to pointed, densely aggregated, spaces between echinae giving microreticulate aspect to some areas of grain surface; 38–42  $\mu\text{m}$ .

Pollen of the extant genus *Acrocomia* is similar to the microfossils in being trichotomocolpate but differs in details of sculpture pattern and wall thickness.

Type 2 (Figs. 24, 25). Reniform; monosulcate, sulcus straight to slightly sinuous, 24  $\mu\text{m}$  long, inner margin faintly dentate, extending entire length of grain; tectate to tectate-perforate, wall ca. 1.5  $\mu\text{m}$  thick; microreticulate (diam. of lumen less than 1  $\mu\text{m}$ ); 28–30  $\mu\text{m}$  by 22–24  $\mu\text{m}$ .

Species within a number of extant genera have pollen similar to the microfossils, including *Aiphanes*, *Chamaedorea* (e.g., *C. caspariana* Klotzsch), *Coccothrinax* [e.g., *C. argentea* (Lodd.) Sang.], and *Copernica*.

Type 3 (Fig. 22). Amb ca. wedge-shaped (widest part of grain above equator); monosulcate, sulcus sinuous, 52  $\mu\text{m}$  long, inner margin entire, extending entire length of grain; tectate to tectate-perforate, wall ca. 1.5  $\mu\text{m}$  thick; finely reticulate, muri smooth, inner margin entire, diam. of lumen ca. equal to width of muri (ca. 1  $\mu\text{m}$  or less); 56–60  $\mu\text{m}$  by 24–28  $\mu\text{m}$ .

Type 4 (Fig. 26). Amb oval (elongated); monosulcate, sulcus straight, 36  $\mu\text{m}$  long, inner margin minutely dentate, extending entire length of grain; tectate, wall ca. 1.5  $\mu\text{m}$  thick; microreticulate (diam. of lumen less than 1  $\mu\text{m}$ ); 39–43  $\mu\text{m}$  by 25–29  $\mu\text{m}$ .

This grain is similar in aperture and sculpture pattern to Type 3, but the widest part of the grain is around the equator and it is considerably smaller.

Type 5 (Fig. 27). Amb ca. wedge-shaped (widest part above equator); monosulcate, sulcus straight, 32  $\mu\text{m}$  long, inner margin dentate, extending entire length of grain; tectate-perforate, wall 2  $\mu\text{m}$  thick; finely reticulate, muri smooth, inner margin entire, lumen ca. 1  $\mu\text{m}$ ; 37–41  $\mu\text{m}$  by 20–24  $\mu\text{m}$ .

#### ANACARDIACEAE

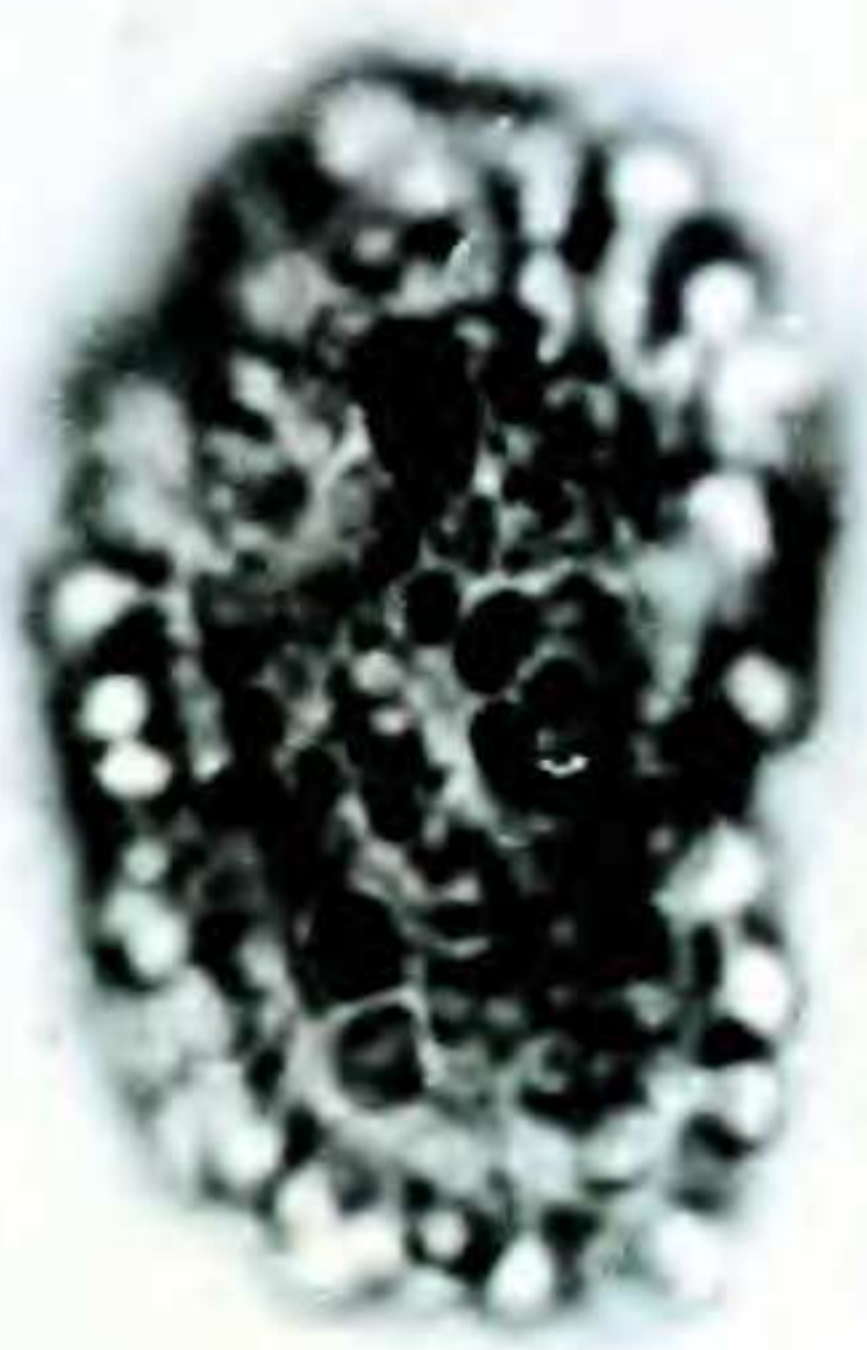
cf. *Camposperma* (Figs. 28, 29). Prolate, amb oval; tricolporate, colpi straight, 18  $\mu\text{m}$  long (apex to equator), narrow, tapering gradually to acute apex, inner margin entire, equatorially arranged, meridionally elongated, equidistant, costae colpi, pores equatorially elongated, 1  $\mu\text{m}$  by 3  $\mu\text{m}$ , situated at midpoint of colpus, inner margin entire; tectate-perforate, wall 1.5  $\mu\text{m}$  thick; finely striato-reticulate; 24–26  $\mu\text{m}$  by 19–21  $\mu\text{m}$ .

The grains are similar to pollen of *Camposperma* and, to some extent, *Comocladia*. *Camposperma* consists of two species with one (*C. panamensis* Standley) native to Panama. They are most abundant in the West Indies and com-

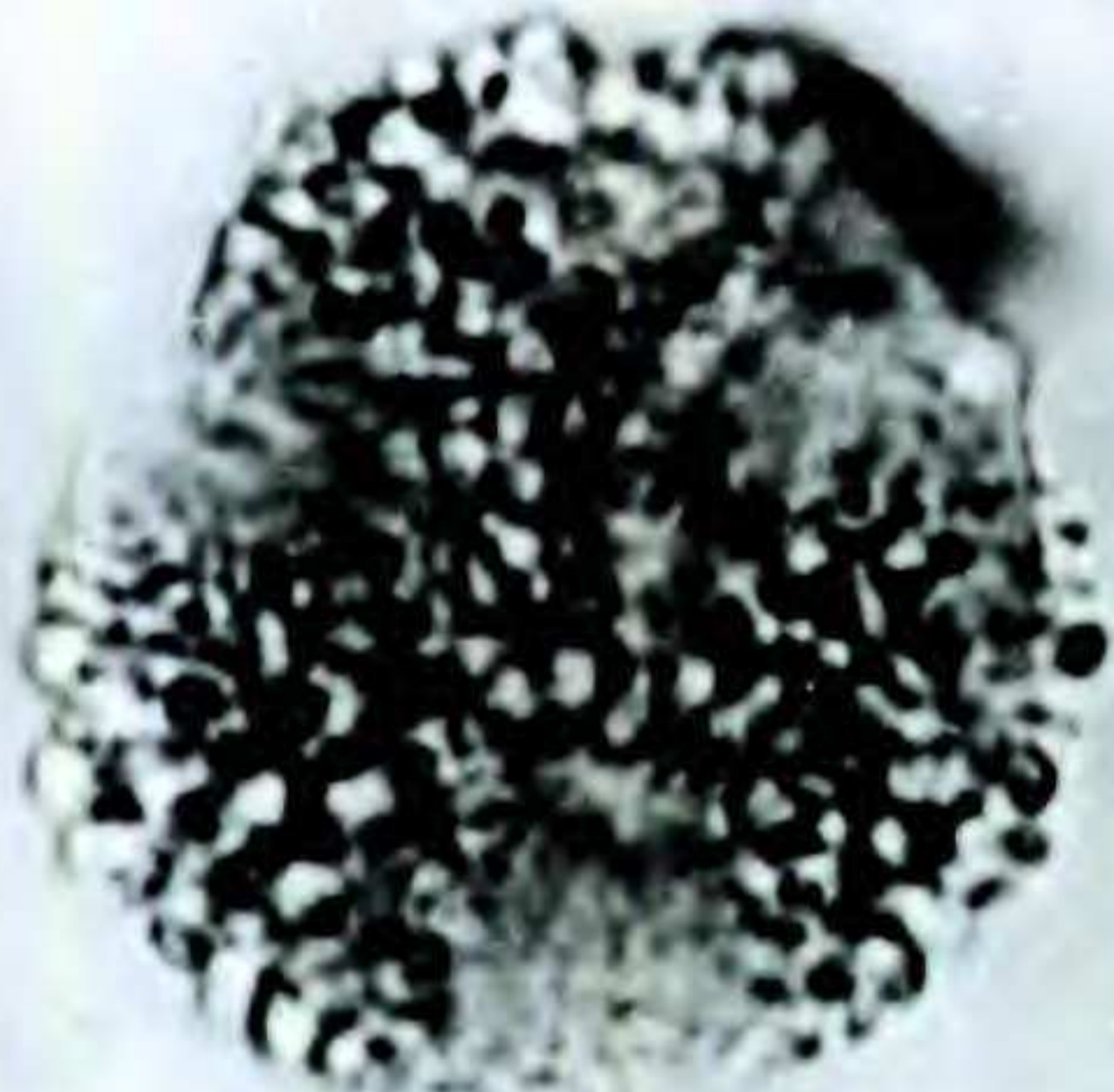
FIGURES 32–53. 32, 33. *Ilex*, equatorial view, 4-1, M-31.—34. *Ilex*, polar view, 9-1, G-23,3.—35. cf. *Paragonia/Arrabidaea*, 4-1, L-7,2.—36, 37. *Combretum/Terminalia*, equatorial view, 4-1, Q-25,4.—38, 39. *Combretum/Terminalia*, polar view, 4-1, U-38,1-2.—40, 41. cf. *Tetragastris*, 4-1, X-8,2.—42–44. cf. *Protium*, 9-1, D-22,1.—45, 46. *Casearia*, 4-1, K-35,2; 4-1, D-21,1.—47, 48, 52, 53. *Lisianthus*, 4-1, X-23; 4-1, V-34,1.—49, 50. cf. *Tontalea*, 9-1, M-38.—51. *Alfaroa/Engelhardia*, 4-1, C-35,1-2.



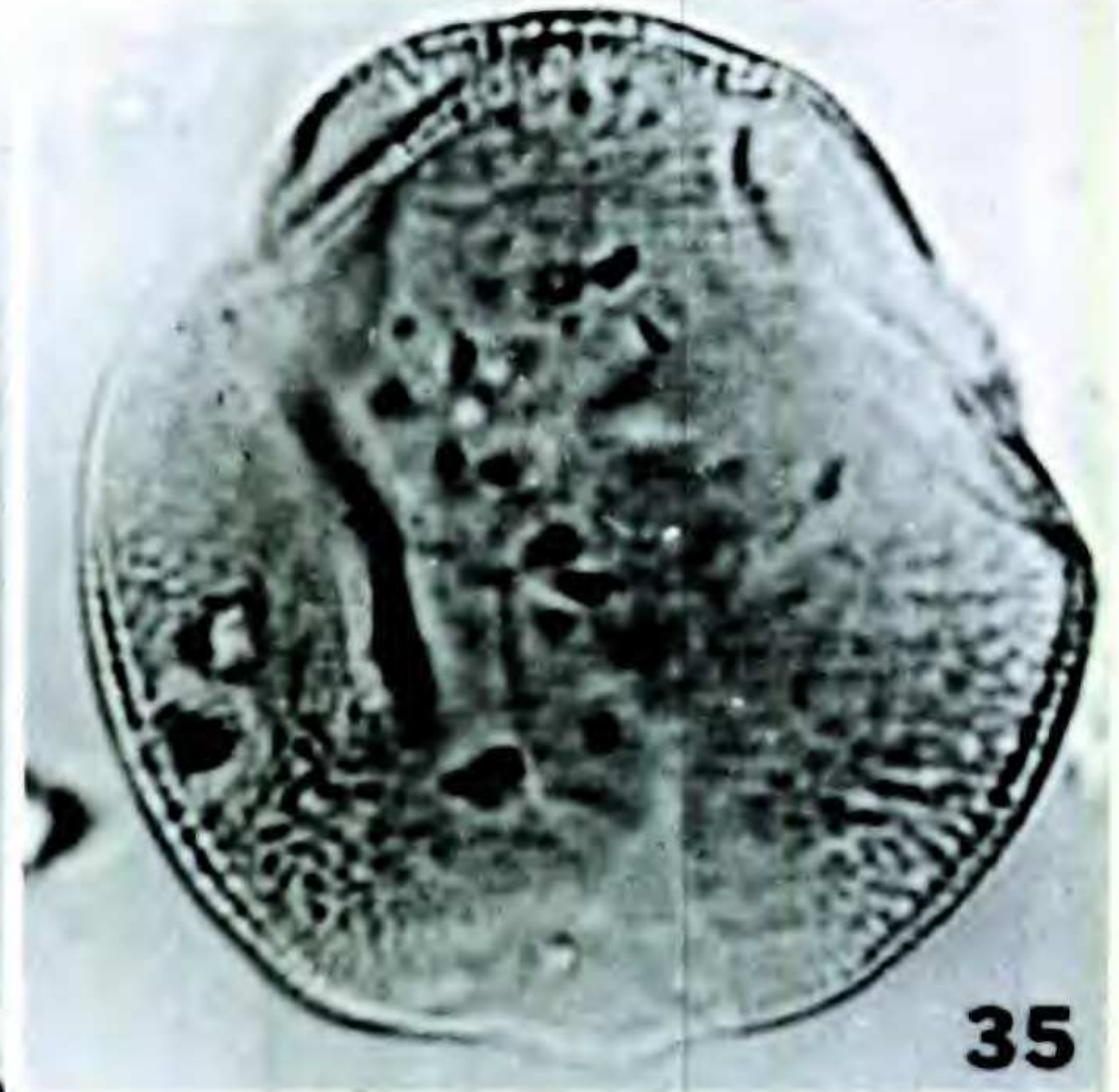
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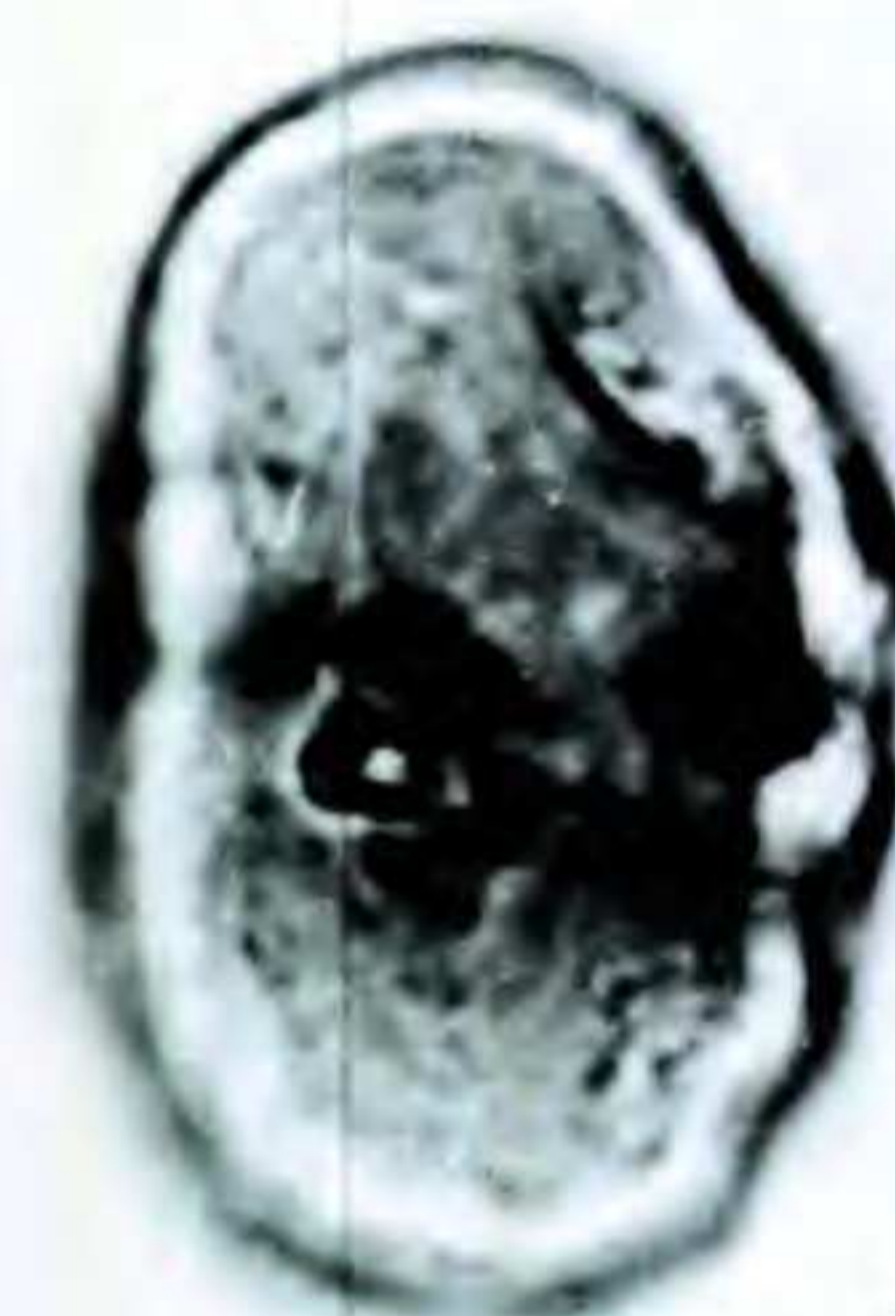
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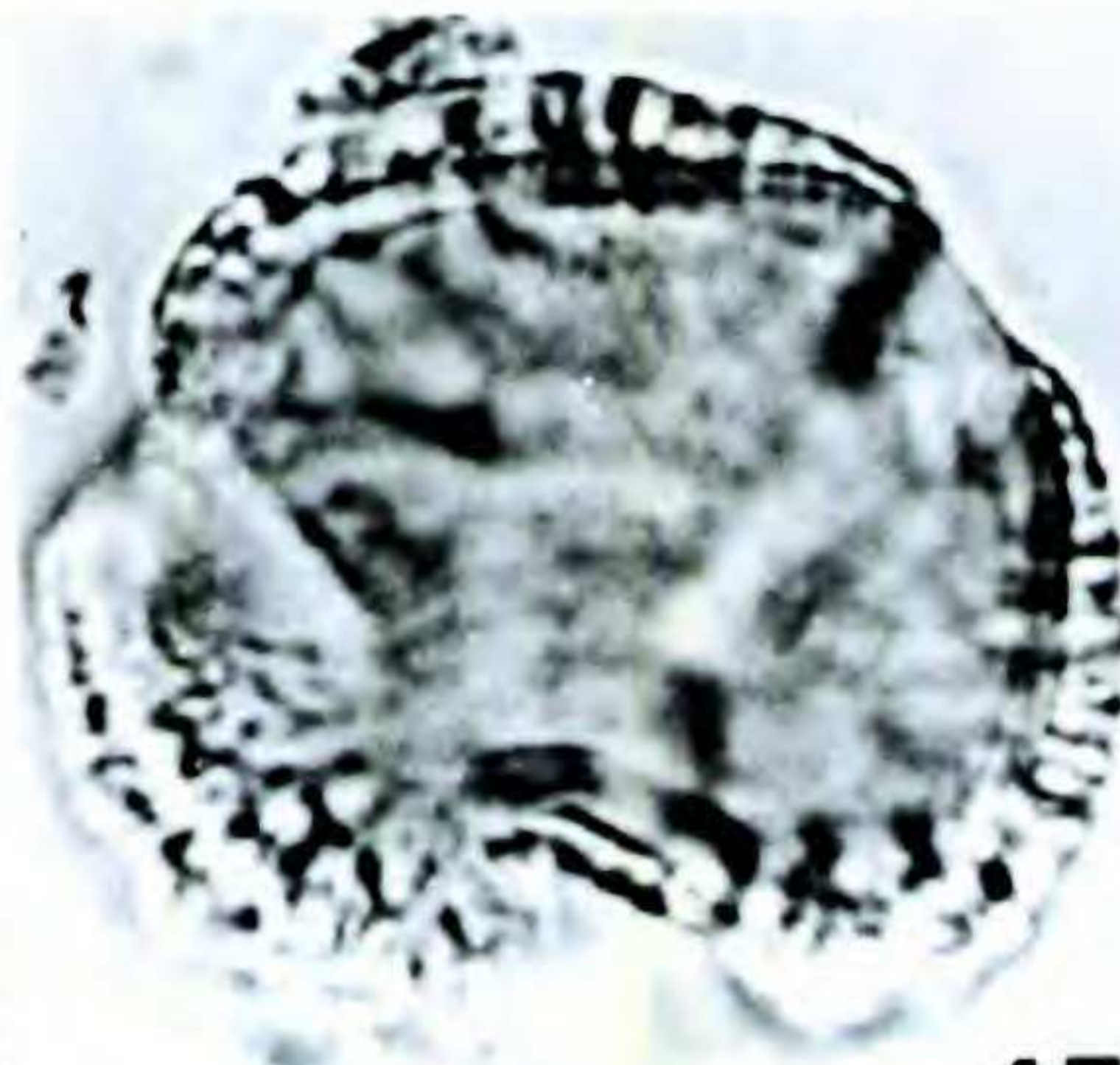
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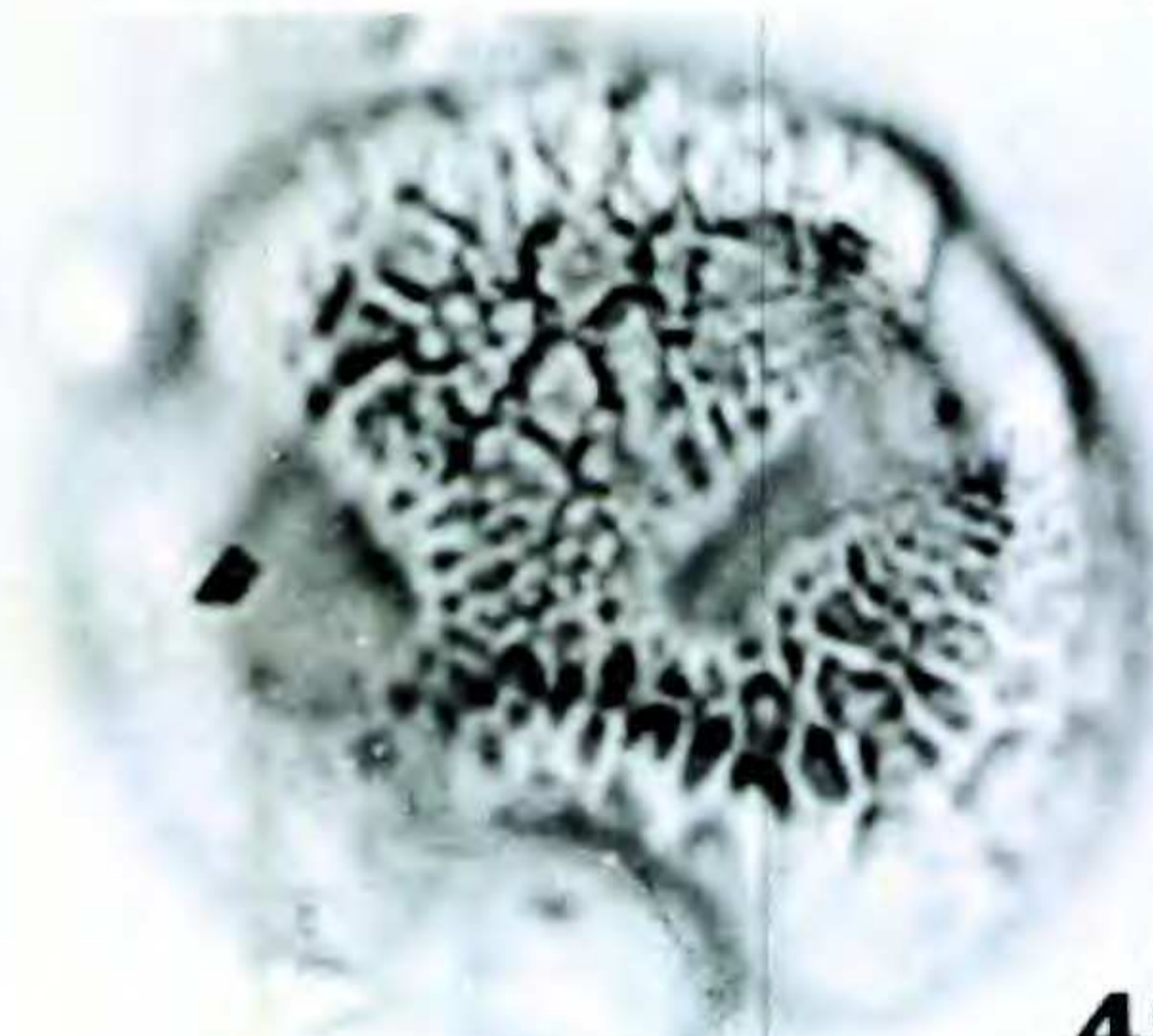
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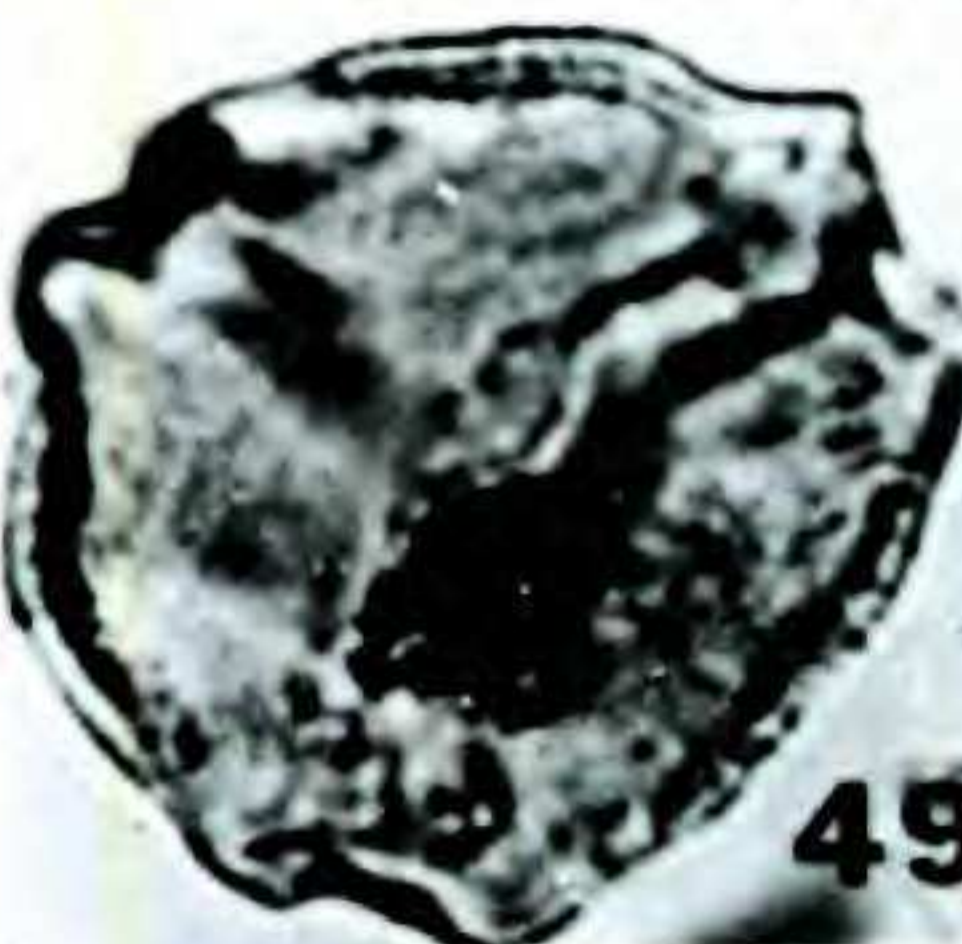
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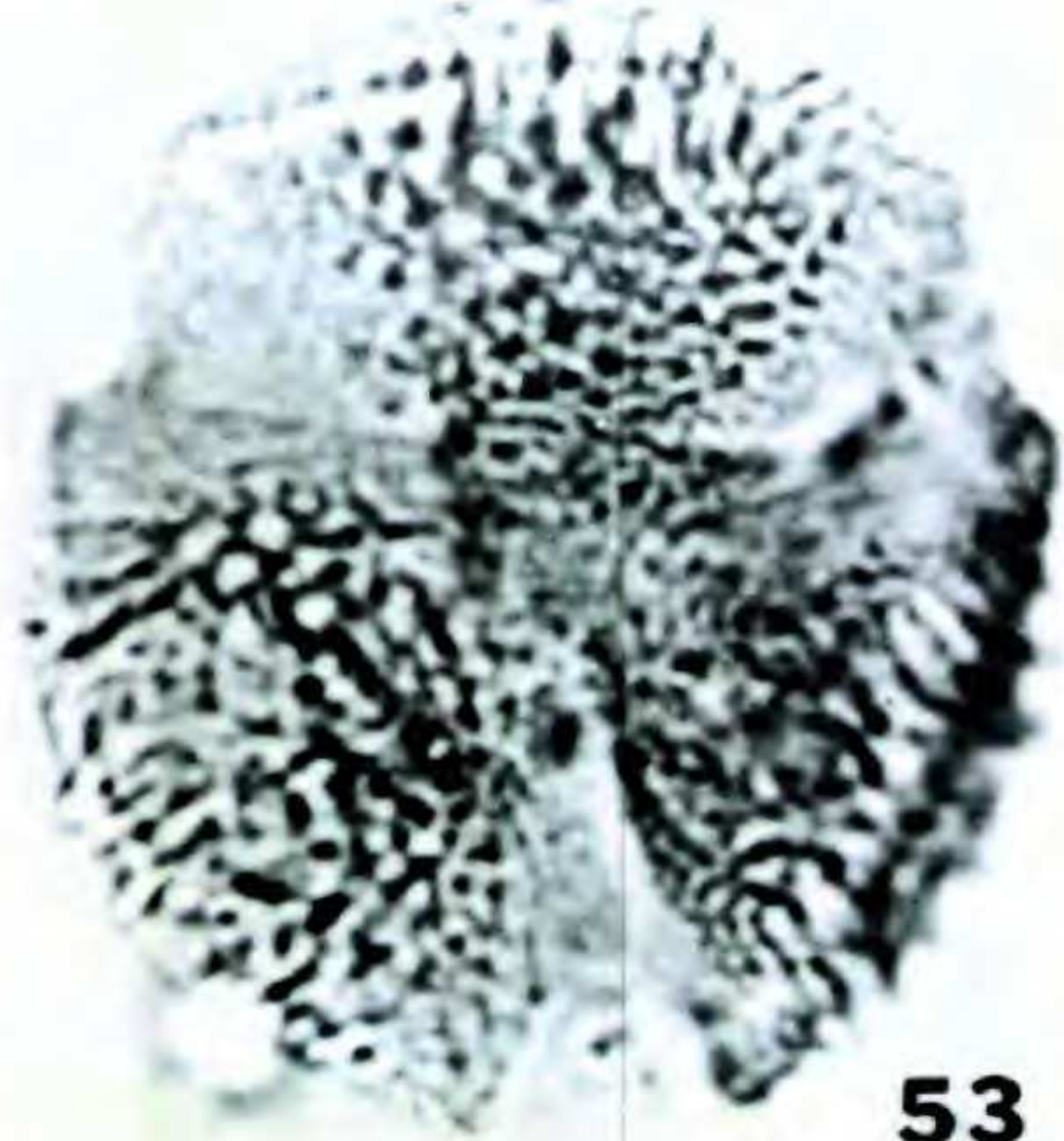
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53

monly grow in lowland, wet habitats such as swamps.

#### AQUIFOLIACEAE

*Ilex* (Figs. 32–34). Oblate-spheroidal, amb circular; tricolporoidate, colpi straight, 10  $\mu\text{m}$  long, broad (ca. 9  $\mu\text{m}$  at midpoint), inner margin diffuse, tapering to acute apex, equatorially arranged, meridionally elongated, equidistant, extending within 6  $\mu\text{m}$  of pole (P.I. 0.27), pores obscure, diam. ca. 2–3  $\mu\text{m}$ , ca. circular, situated at midpoint of colpus; intectate, wall thickness (viz., height of columellae) 3  $\mu\text{m}$ ; clavate; 25–32  $\mu\text{m}$ .

*Ilex* is a widespread genus of about 400 species. In Latin America it commonly occurs in mesic to slightly drier habitats. For example, in the Antilles it grows in the high-altitude pine forests (Howard, 1973); in Veracruz it is a member of the low evergreen selva, the high semi-evergreen selva, and the bosque caducifolio (Gomez-Pompa, 1973); and in Panama it is found at mid-altitudes in drier forest habitats and late secondary forests (Porter, 1973).

Fossil pollen of *Ilex* appears in the early Late Cretaceous of Australia, late Late Cretaceous of North America, and Paleocene of South America (Muller, 1981). By Tertiary times it is virtually cosmopolitan. In northern Latin America *Ilex* is known from the Eocene of Panama (this report), the Oligocene of Puerto Rico (Graham & Jarzen, 1969), the Miocene of Veracruz, Mexico (Graham, 1976), the Miocene of Panama (Graham, 1985), and the Quaternary of Panama (Bartlett & Barghoorn, 1973).

#### CF. ARALIACEAE (FIGS. 30, 31)

Prolate to prolate-spheroidal, amb circular; tricolporate, colpi straight, 10  $\mu\text{m}$  long, inner margin entire, tapering to acute apex, equatorially arranged, meridionally elongated, equidistant, pore obscure, slightly elongated equatorially, ca. 1–1.5  $\mu\text{m}$  by 2.5  $\mu\text{m}$ , situated at midpoint of colpus; tectate-perforate, wall 1.5–2  $\mu\text{m}$  thick; finely reticulate; 21–24  $\mu\text{m}$ .

The primary purpose of including this microfossil is to document the occurrence of Araliaceae-type pollen in the assemblage, even though the specimens cannot be identified to genus.

#### BIGNONIACEAE

cf. *Paragonia/Arrabidaea* (Fig. 35). Oblate, amb circular; tricolporate, colpi straight, 18  $\mu\text{m}$

long, broad (ca. 10  $\mu\text{m}$  at equator), equatorially arranged, meridionally elongated, equidistant, tapering to acute apex, margin diffuse; tectate to tectate-perforate, wall ca. 1.5  $\mu\text{m}$  thick; finely reticulate; 45  $\mu\text{m}$ .

Modern pollen of the Bignoniaceae has been studied by Gentry and Tomb (1979). Based on their survey, and material in our reference collection, the microfossil is most similar to *Paragonia* [*P. pyramidata* (Rich.) Bur.] and to *Arrabidaea* [e.g., *A. corallina* (Jacq.) Sandw.]. One collection of *Paragonia* (Croat 7895, BCI, Panama, MO) is especially similar in being relatively large, thin-walled, and having a diffuse colpus margin. Pollen from two other collections (Harvard exchange) differ in being smaller, thick-walled, and with distinct costae colpi.

*Arrabidaea* and *Paragonia* are both lianas distributed from Mexico to Brazil, Bolivia, and the former to Argentina. *Paragonia* is widespread in the tropical moist and wet forests of Panama. Both *Arrabidaea* and *Paragonia* produce numerous flowers in terminal panicles and are among the most common bignoniaceous vines in Panama. *Paragonia* “flowers in extravagant bursts lasting about a month, abundantly in the dry season and erratically throughout the year” (Croat, 1978: 768), and the various *Arrabidaea* species have similar flowering peaks spaced throughout the year (Gentry, 1974). These features are consistent with small percentages in the fossil record (1% or less, Table 1) even though the genera are insect-pollinated lianas of the forest canopy.

#### BURSERACEAE

The two principal neotropical genera of the Burseraceae are distinguished palynologically by the striato-reticulate pollen of *Bursera* (ca. 80 species) and the psilate pollen of *Protium* (ca. 90 species). Within the latter, however, there are other smaller genera with similar pollen (e.g., *Crepidospermum*, 2 species; *Hemicrepidospermum*, 1 species; *Tetragastris*, 8–12 species). Two subtypes of this prolate, psilate pollen are recognized in the Gatuncillo assemblage. One is comparatively thick-walled and is most similar to pollen of *Protium*. The other is thin-walled with a more hyaline appearance and is comparable to *Tetragastris*. Because there is some overlap in pollen morphology among these modern genera, however, the fossils are referred to cf. *Protium* and cf. *Tetragastris*.

cf. *Tetragastris* (Figs. 40, 41). Prolate; tri-

colporate, colpi narrow, straight, ca. 25  $\mu\text{m}$ , inner margin entire, sides parallel, apex acute, equatorially arranged, meridionally elongated, equidistant, distinct costae colpi and costae pori 4  $\mu\text{m}$  thick in equatorial region surrounding pore, pore elongated equatorially, 2.5  $\mu\text{m}$  by 6  $\mu\text{m}$ , situated at midpoint of colpus, inner margin entire; tectate, exine relatively thin (1.5  $\mu\text{m}$ ); psilate, hyaline; 32  $\mu\text{m}$  by 24  $\mu\text{m}$ .

*Tetragastris* is a tree or shrub distributed from Brazil northward through the Antilles (to Hispaniola) and Central America to British Honduras. The most common species is *T. panamensis* (Engl.) O. Kuntze found in British Honduras, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, the Guianas, Brazil, and Peru. It is widespread in Panama and Porter (1970), citing Johnston (1949), noted that it is "an important forest tree on San Jose Island, where it may make up more than half of the canopy layer . . . ." According to Croat (1978), the species is ecologically variable and ranges from tropical moist to tropical dry forests. There are no other reports of *Tetragastris* in the fossil record.

cf. *Protium* (Figs. 42–44). Prolate; tricolporate, colpi narrow, faint, straight, ca. 26  $\mu\text{m}$ , inner margin entire, sides parallel, apices acute, equatorially arranged, meridionally elongated, equidistant, costae colpi and costae pori 3.5  $\mu\text{m}$  thick in equatorial region surrounding pore, pore equatorially elongated (colpi transversalis), 2.5  $\mu\text{m}$  by 8  $\mu\text{m}$ , situated at midpoint of colpus, inner margin entire; tectate, wall 2.5  $\mu\text{m}$  thick; psilate; 36  $\mu\text{m}$  by 24  $\mu\text{m}$ .

*Protium* is a tree or shrub of the tropical forests of both the New and Old Worlds. In the neotropics it is most common in South America, with seven species listed for Panama (Porter, 1970). Throughout Central America it occurs in the tropical moist, premontane wet, and tropical wet forests. The fossil record of the Burseraceae is poorly known, with tentative reports that may extend the range of the family back to the lower Eocene (Muller, 1981). In the Caribbean area, *Protium*-type pollen is recorded from the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976).

#### COMBRETACEAE

*Combretum/Terminalia* (Figs. 36–39). Prolate to prolate-spheroidal, amb circular (lobate reflecting arrangement of apertures); tricolporate with 3 pseudocolpi, colpi straight, ca. 22–25  $\mu\text{m}$ ,

inner margin entire, narrow, sides parallel for most of length, then tapering near terminus to acute apex, equatorially arranged, meridionally elongated, equidistant, extending within 5  $\mu\text{m}$  of pole (P.I. 0.2), pore (endoaperture) frequently obscure, circular, diam. ca. 3  $\mu\text{m}$ , situated at midpoint of colpus; tectate, wall 1.5  $\mu\text{m}$  thick; psilate to faintly scabrate; 25–30  $\mu\text{m}$  by 18–22  $\mu\text{m}$ .

The microfossils oriented in polar view (Figs. 38, 39) are most similar to *Combretum/Terminalia* pollen because the pore is more evident. Some microfossils oriented in equatorial view (Figs. 36, 37) are comparable in size, shape, sculpture, structure, and in the presence of multiple apertures (colpi), but the pore is obscure. In the pollen of most modern species of *Combretum/Terminalia* the pore is visible in equatorial view, but occasionally it is less obvious. The grain illustrated in Figures 38 and 39 is typical of *Combretum/Terminalia*, while those represented by Figures 36 and 37 are regarded as likely belonging to the same complex.

It is not possible to consistently distinguish *Combretum* and *Terminalia* pollen under light microscopy when they are encountered as isolated microfossils (Graham, 1980); hence, the designation *Combretum/Terminalia*. Similar pollen occurs in the Melastomataceae, but it is either smaller (9–15  $\mu\text{m}$ ) and/or has distinct costae colpi.

Both *Combretum* and *Terminalia* are widespread in Latin America and most commonly occur in wet to moist forests, although *C. fruticosum* (Loeff.) Stunz can range into drier habitats. The microfossils are also known from the Miocene of Veracruz, Mexico (Graham, 1976) and from the Quaternary of Panama (as *Combretum*; Bartlett & Barghoorn, 1973). Muller (1981) cited other occurrences that extend the complex into the upper Eocene of Cameroon, and it is now known also from the upper Eocene of Panama (this report). If this is the approximate complete stratigraphic range of *Combretum/Terminalia*, it may explain the difficulty in identifying certain types from the Gatuncillo assemblage, because the group would be in its early stage of differentiation.

#### FLACOURTIACEAE

*Casearia* (Figs. 45, 46). Prolate; tricolporate, colpi narrow, straight, 22–24  $\mu\text{m}$ , inner margin faintly undulating, apices acute, equatorially arranged, meridionally elongated, equidistant, nar-

row costae colpi, pore equatorially elongated (colpi transversalis), 2  $\mu\text{m}$  by 5  $\mu\text{m}$ , situated at midpoint of colpus, inner margin entire; tectate, wall 1.5  $\mu\text{m}$  thick; microreticulate; 30–35  $\mu\text{m}$  by 22–25  $\mu\text{m}$ .

*Casearia* includes about 250 species of trees and shrubs widely distributed in tropical to subtropical regions of both hemispheres. Eight species are listed for Panama (Robyns, 1968), and these generally occur in moist forest types, although some (e.g., *C. arguta* H.B.K., *C. commersoniana* Camb.) range into the drier premontane or tropical dry forests (Croat, 1978). Pollen morphology of the family has been studied by Keating (1973). The fossil pollen is most similar to *C. sylvestris* Sw. In the Caribbean region, *Casearia* has been reported from the Oligocene of Puerto Rico (Graham & Jarzen, 1969) and the upper Miocene of Veracruz, Mexico (Graham, 1976). The present report from the Gatuncillo Formation extends the fossil record to the upper Eocene.

#### GENTIANACEAE

*Lisianthus* (Figs. 47, 48, 52, 53). Oblate to oblate-spheroidal, amb circular; tricolporate, colpi broad at equator, tapering to acute apex, ca. 18  $\mu\text{m}$  long (equator to apex), extending within 6–7  $\mu\text{m}$  of pole (P.I. 0.02), equatorially arranged, meridionally elongated, equidistant, inner margin entire to slightly diffuse, faint margo formed by gradual diminution of reticulum near colpus margin, pore circular, 4–5  $\mu\text{m}$ , situated at midpoint of colpus, margin diffuse; tectate-perforate, height of columellae 2.5  $\mu\text{m}$  in equatorial mesocolpal region, diminishing toward poles and margins of colpi; reticulate, reticulum somewhat irregular, diam. of lumen ca. 2–3  $\mu\text{m}$  in equatorial mesocolpal region, diminishing toward poles and margins of colpi, muri tall (ca. 2.5  $\mu\text{m}$ ) in equatorial mesocolpal area, giving boxwork effect to reticulum, muri surface psilate, margins entire; 35–45  $\mu\text{m}$ .

The presence of *Lisianthus* pollen in the Gatuncillo Formation has been reported earlier (Graham, 1984). The plants grow from south-central Mexico, through the Antilles and Central America, into northwest Colombia (Weaver,

1972; Elias & Robyns, 1975). They are found in a variety of habitats including secondary scrub, pine forests, cloud forests, and savannahs ranging from sea level to about 1,800 m. Of particular interest from the standpoint of the fossil pollen record is that, although primarily insect-pollinated, many species are highly floriferous and occur in dense stands at moderately low elevations. Fossils of the Gentianaceae are known from the lower Eocene of Texas, and other records extend its range into the Paleocene (Crepet & Daghljan, 1981). The Gatuncillo material represents the first report of *Lisianthus* in the fossil record.

#### HIPPOCRATIACEAE

cf. *Tontalea* (Figs. 49, 50). Oblate, amb ca. circular, undulating; tricolporate, colpi narrow, straight, 12  $\mu\text{m}$  long, inner margin minutely dentate, apices acute, extending within 3–4  $\mu\text{m}$  of pole (P.I. 0.015), equatorially arranged, meridionally elongated, equidistant, narrow margo, pore circular, 3  $\mu\text{m}$ , situated at midpoint of colpus; tectate to tectate-perforate, ectexine thicker (columellae longer) in equatorial mesocolpal area (ca. 2  $\mu\text{m}$ ), thinning toward apertures (1.5  $\mu\text{m}$ ); finely reticulate; 26  $\mu\text{m}$ .

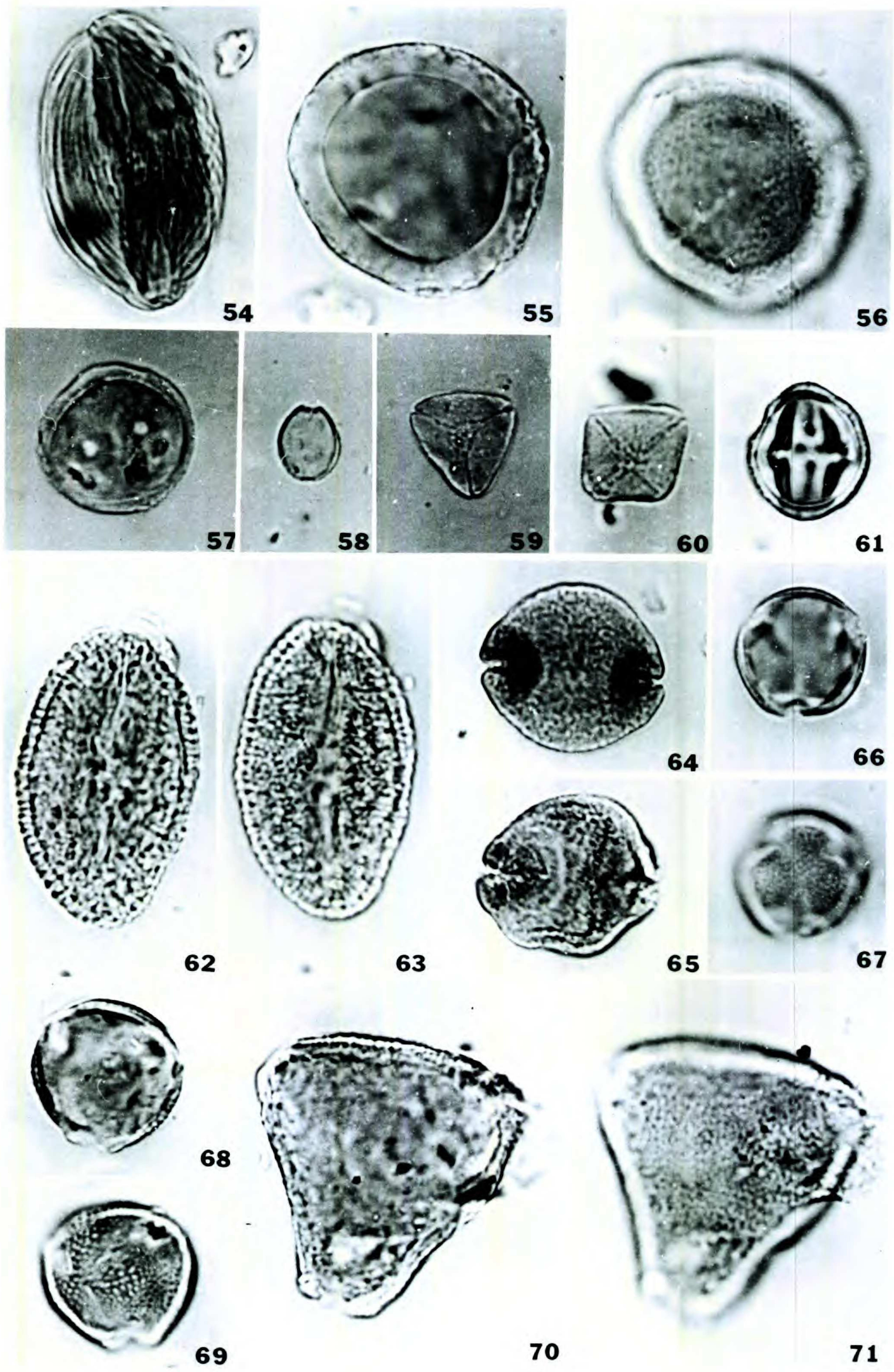
*Tontalea* is a neotropical genus consisting of about 31 species of lianas, slender shrubs, or small trees. Only one [*T. richardii* (Pery.) A. C. Smith] occurs in Panama (Dodson & Robyns, 1965). This species is a liana common in the upper canopy of the tropical moist forest, although it is occasionally found at lower elevations and along the coast (Croat, 1978). Two other genera in the family contain species with pollen generally similar to *Tontalea* (*Cueruea*, *Pristimera*), but in the fineness of the reticulum and in wall structure (columellae) as seen in optical section, the fossil pollen is most similar to *Tontalea*. The genus has not previously been reported in the fossil record.

#### JUGLANDACEAE

*Alfaroa/Engelhardia* (Fig. 51). Oblate, amb oval-triangular; triporate, pore circular, ca. 2  $\mu\text{m}$ , inner margin entire, equatorially arranged, equi-

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FIGURES 54–71. 54. *Crudia*, 2-1, T-21,1-3.—55, 56. Malpighiaceae type 1, 4-1, C-22.—57. Malpighiaceae type 2, 9-1, H-45,3.—58. cf. *Ficus*, 4-1, W-12,1-2.—59. *Eugenia/Myrcia*, 2-1, E-30,3.—60. *Eugenia/Myrcia* tetra-aperturate form, 4-1, V-24.—61. *Rhizophora*, 4-1, K-24,1.—62, 63. *Coccoloba*, 4-1, X-7,2-4.—64, 65. *Faramea*, 2-1, G-14,2; 9-1, K-39,4.—66, 67. Rubiaceae type 1, 4-1, G-17,1-3.—68, 69. Rubiaceae type 2, 4-1, S-14.—70, 71. *Paullinia*, 4-1, V-11,1-2.



distant; tectate, wall  $1.5\ \mu\text{m}$  thick; psilate to faintly scabrate;  $26\ \mu\text{m}$ .

Whitehead (1965) and Nichols (1973) conclude that *Engelhardia* and *Alfaroa* cannot consistently be distinguished on the basis of pollen morphology. Crepet et al. (1980) noted that one exception may be the distinctly smaller and triangular pollen of section *Psilocarpeae* of *Engelhardia*. Since our Gatuncillo material is not of this type, it is referred to *Alfaroa/Engelhardia*. Similar pollen is stratigraphically and geographically widespread throughout the Caribbean Tertiary and is a common microfossil in temperate regions of the northern hemisphere (Muller, 1981; Crepet et al., 1980). The fossil pollen is frequently referred to the form-genus *Momipites*. It is known from the Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969), the Oligo-Miocene of Chiapas, Mexico (Langenheim et al., 1967), and the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976). In the Gatuncillo material the pollen is rare (three grains encountered among the three samples studied). Both *Alfaroa* and *Engelhardia* occur in Central America (Manning, 1960) and are typically, but not exclusively, associated with temperate forests.

#### LEGUMINOSAE/CAESALPINIOIDEAE

*Crudia* (Fig. 54). Prolate; tricolporoidate; colpi narrow, straight,  $22\text{--}38\ \mu\text{m}$ , frequently obscured by sculpture elements, extending nearly entire length of grain, equatorially arranged, meridionally elongated, equidistant, pore area faint, ca. circular, situated at midpoint of colpus; tectate, but with occasional separations between sculpture elements, wall  $1.5\ \mu\text{m}$  thick; distinctly and coarsely striate, striae generally oriented parallel to long axis of grain, surface psilate, margins entire, occasionally appearing beaded from underlying pores in foot layer/endexine;  $42\ \mu\text{m}$  by  $27\ \mu\text{m}$ .

In the Caesalpinioideae 12 genera have striate pollen, but only two of these (*Crudia*, *Macrobium*) are closely similar to the microfossils and occur in the New World. The genus *Macrobium* has about 60 species that grow in tropical America. The pollen of these differ from the fossil in having more coarse, thick striations and/or with a much more conspicuous beaded appearance to the striations imparted by the underlying pores. The genus *Crudia* has about 55 species with ten growing in the neotropics. These are mainly Amazonian and often riverine species

(Cowan & Polhill, 1981: 131; pollen morphology, Graham & Barker, 1981). *Crudia*-type pollen (under the form-genus name *Striatocolpites catatumbus* Gonzalez) is known back to the Eocene in northern South America and to the Paleocene in Nigeria (Muller, 1981).

#### MALPIGHIACEAE

Pollen of the Malpighiaceae is distinctive, but within the family generic identifications are difficult. Fossil pollen is common, but at low frequencies, in the Caribbean Tertiary. In the Gatuncillo Formation two pollen types belonging to the Malpighiaceae are present, but these cannot be referred to any one genus in the family.

Type 1 (Figs. 55, 56). Spherical, amb circular; pericorporate, colpi ca. straight to slightly sinuous, narrow,  $22\text{--}24\ \mu\text{m}$ , apices acute, inner margin minutely dentate, pores oval to slit-like, long axis at right angle to colpus,  $1\ \mu\text{m}$  by  $3.5\ \mu\text{m}$ , situated at midpoint of colpus, inner margin entire to minutely dentate; tectate, wall conspicuously thick ( $5\ \mu\text{m}$ ); minutely punctate-microreticulate;  $44\ \mu\text{m}$ .

Type 2 (Fig. 57). Spherical, amb circular; pericorporate, colpi straight, narrow, short ( $2\text{--}4\ \mu\text{m}$ ), faint, pores conspicuous, circular to oval,  $2.5\ \mu\text{m}$ , situated at midpoint of colpus, inner margin entire, distinct annulus ca.  $2.5\ \mu\text{m}$  wide; tectate, wall  $3\ \mu\text{m}$  thick; scabrate;  $27\ \mu\text{m}$ .

#### MORACEAE

cf. *Ficus* (Fig. 58). Prolate, amb oval; diporate, pores ca. circular, ca.  $1.5\ \mu\text{m}$ , situated at apices of grain; tectate, wall ca.  $1.5\ \mu\text{m}$  thick; scabrate;  $10\ \mu\text{m}$  by  $13\ \mu\text{m}$ .

In most diporate Moraceae pollen the pores are equatorial, frequently with an annulus, and are more spherical than the microfossil with a somewhat thicker wall. The fossil pollen is most similar to *Ficus*, but generic distinctions are so subtle that the microfossils are referred to cf. *Ficus*. The genus is large (ca. 1,000 species worldwide) and poorly understood taxonomically. In Panama, *Ficus* is most commonly associated with the moist forest type but can range into drier habitats. As expected from the pollination mechanism and floral structure, pollen of cf. *Ficus* is rare in the Gatuncillo palynoflora. In the stratigraphic literature the pollen type is known as *Psiladiporites minimus* van der Hammen & Wymstra and ranges from lower Miocene to Recent (Germeraad et al., 1968). The Gatuncillo

occurrence extends the range back to the upper Eocene.

#### MYRTACEAE

*Eugenia/Myrcia* (Figs. 59, 60). Oblate to peroblate, amb triangular; tricolporate, colpi narrow, straight, 10–12  $\mu\text{m}$ , inner margin slightly dentate, equatorially arranged, meridionally elongated, equidistant, syncolpate, pores ca. 1  $\mu\text{m}$ , situated on equator at midpoint of colpus; tectate, wall thin (ca. 1.5  $\mu\text{m}$ ), faintly scabrate; 17–19  $\mu\text{m}$ .

Pollen of *Eugenia* and *Myrcia* is similar, and it is not possible to consistently refer isolated microfossils to either genus (Graham, 1980). This pollen type is common in Gulf/Caribbean Tertiary deposits, ranging from the middle Eocene (Elsik & Dilcher, 1974) to Recent. An occasional tetracolporate form is encountered (Fig. 60), and these are matched by modern species that include some multiaperturate pollen [e.g., *E. rhombea* (Berg.) Krug & Urb.]. The modern genera are important components of neotropical vegetation but collectively range through a wide variety of habitats which reduces their usefulness in paleoecological reconstructions.

#### POLYGONACEAE

*Coccoloba* (Figs. 62, 63). Prolate; tricolporate, colpi narrow, straight, extending nearly entire length of grain, 30–38  $\mu\text{m}$  long, apices acute, inner margin entire, equatorially arranged, meridionally elongated, equidistant, costae colpi, pore (endoaperture) frequently obscure, ca. circular, 2–3  $\mu\text{m}$ , situated at midpoint of colpus; tectate-perforate, wall thick (3  $\mu\text{m}$ ), columellae thick and clearly evident in optical section, sexine (tops of columellae) distinct from nexine (foot layer); reticulate, diam. of lumen ca. 1  $\mu\text{m}$ ; 39–50  $\mu\text{m}$  by 23–36  $\mu\text{m}$ .

*Coccoloba* is common in moist forest types of tropical America. Howard (1960) recognized 12 species for Panama, and several of these range into lowland coastal habitats where pollen can readily be incorporated into accumulating sediments. Microfossils are common in the Gatuncillo Formation (3.5% in sample 4; 2% in sample 9; Table 1), and in the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976). The Eocene specimens from Panama cannot be related to a single modern species but are quite similar to *C. belizensis* Standley.

#### RHIZOPHORACEAE

*Rhizophora* (Fig. 61). Prolate to prolate-spheroidal; tricolporate, colpi narrow, straight, 14–16  $\mu\text{m}$ , apices acute, equatorially arranged, meridionally elongated, equidistant, costae colpi ca. 3  $\mu\text{m}$ , pores elongated equatorially (colpi transversalis), 1  $\mu\text{m}$  by 4  $\mu\text{m}$ , constricted at midpoint of colpus, inner margin entire; tectate-perforate, wall thick (2–3  $\mu\text{m}$ ); finely reticulate; 19–21  $\mu\text{m}$  by 22–24  $\mu\text{m}$ .

Fossil pollen of *Rhizophora*, also listed in the literature under the form-genus name *Zonocostites*, is almost by definition an important component of Tertiary lignites in warm-temperate to subtropical regions that form under coastal, brackish-water conditions (Cohen & Spackman, 1972; Scholl, 1964a, 1964b). Pollen of the six species (and one hybrid) are similar, but sufficient differences exist to tempt species distinctions in the fossil record. Modern and fossil pollen of *Rhizophora* was studied by Langenheim et al. (1967), Leopold (1969), and Muller and Caratini (1977). The last authors concluded that three groups of species can be recognized on the basis of pollen morphology: *R. mucronata/stylosa*; *R. apiculata/lamarckii/mangle*; and *R. racemosa*.

The microfossils in the upper Eocene Gatuncillo Formation are difficult to identify because they are near the apparent time of early diversification and radiation of the genus. The oldest known records are from the lower to middle Eocene of southeast Asia (Muller & Caratini, 1977), and the genus first appears in tropical America in the late Eocene (viz., Gatuncillo time). As a result, there are a number of microfossils in our Panama material that appear similar to *Rhizophora* but are quite small (14–16  $\mu\text{m}$  by 18–20  $\mu\text{m}$ ) and sufficiently close to spherical as to orient in various views, precluding determining exact shape and/or aperture morphology. Many 'unknowns' in this category represent *Rhizophora*-like pollen and may be early forms of the pollen in these tropical American sediments. The specimen in Figure 61 is a more typical example of *Rhizophora* in the Gatuncillo Formation.

#### RUBIACEAE

*Faramea* (Figs. 64, 65). Oblate, amb oval; diporate, pores (short colpi) 6–7  $\mu\text{m}$  (apex to equator), inner margin entire, apices ca. rounded, situated at poles (apices of long axes), broad diffuse costae pori (colpi) 4–5  $\mu\text{m}$  wide, giving



stained effect to region surrounding aperture; tectate-perforate, wall ca. 1  $\mu\text{m}$  thick; finely reticulate; 27–30  $\mu\text{m}$  by 24–30  $\mu\text{m}$ .

*Faramea* is a genus of about 125 species of trees and shrubs widely distributed in the Antilles, Central America, and South America (Dwyer, 1980). The pollen is typically triporate and reticulate, common to the family Rubiaceae, and these pollen types have been recorded from the Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969) and the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976). Among the species with normal triporate pollen, however, are some in our reference collection (e.g., *F. coarinnensis* Muell. Arg.) in which many of the grains are diporate. The Gatuncillo specimens are all of the diporate type. Consequently, the known stratigraphic range of the genus is upper Eocene to Recent, but the diporate form is known only from the upper Eocene, and the triporate type ranges from the middle Oligocene to Recent. The present report extends the range back into the Eocene from that reported in Muller (1981).

Pollen of the Rubiaceae is abundant in the Gatuncillo Formation, but it frequently belongs to a generalized type common to many genera in the family. Two of the more common forms are described below.

Type 1 (Figs. 66, 67). Oblate to oblate-spheroidal, tricolporate, colpi short (6–8  $\mu\text{m}$ ), broad (ca. 4  $\mu\text{m}$  at equator), tapering to ca. acute apex, inner margin entire, equatorially arranged, meridionally elongated, equidistant, pore elongated equatorially (colpi transversalis), 1  $\mu\text{m}$  by 4  $\mu\text{m}$ , situated at midpoint of colpus; tectate-perforate, wall ca. 1  $\mu\text{m}$ , slightly thicker in mesocolpal region; finely reticulate; 18–23  $\mu\text{m}$ .

This pollen type is common to several genera of the Rubiaceae, including especially *Antirrhoea*, but also *Calycophyllum*, *Erithalis*, and others.

Type 2 (Figs. 68, 69). This rubiaceous grain is similar to Type 1, except it is slightly larger (26  $\mu\text{m}$  versus 18–23  $\mu\text{m}$ ) and more distinctly reticulate.

## SAPINDACEAE

*Cardiospermum* (Fig. 72). Oblate, amb triangular; triporate, pores protruding ca. 3–4  $\mu\text{m}$ , 1–2  $\mu\text{m}$  diam., equatorially arranged, equidistant, aspidate, vestibulate; tectate-perforate, wall relatively thin (ca. 1.5  $\mu\text{m}$ ); reticulate, muri equal to or slightly broader than diameter of lumen, giving punctate effect to portions of the exine; 45  $\mu\text{m}$ .

*Cardiospermum* is a genus of about 14 species of herbaceous, annual or perennial vines widely distributed in tropical America and in Africa. Two species are currently known from Panama (*C. grandiflorum* Swartz, *C. microcarpum* H.B.K.), and another (*C. halicacabum* L.) likely occurs there (Croat, 1976). As noted by Muller (1981), *Cardiospermum* pollen has been mentioned in the Tertiary fossil record (e.g., Leopold & MacGinitie, 1972, Eocene, Rocky Mountain region) but without documentation (description or illustration). Bartlett and Barghoorn (1973) record the genus from the Quaternary of Panama.

*Paullinia* (Figs. 70, 71). Oblate, amb triangular; triporate, pores 3–4  $\mu\text{m}$ , equatorially arranged, equidistant; tectate-perforate, wall 2–3  $\mu\text{m}$  thick; finely reticulate; 45  $\mu\text{m}$ .

*Paullinia* is a genus of scandent shrubs or lianas widely distributed in tropical America, with one species in Africa (*P. pinnata* L.). It is most characteristic of moist forest types. About 194 species are listed for the neotropics, and Croat (1976) recorded 37 for Panama. Pollen of the genus is known from the upper Miocene of Veracruz, Mexico (Graham, 1976) and from the Quaternary of Panama (Bartlett & Barghoorn, 1973). The Gatuncillo occurrence extends the stratigraphic record of *Paullinia* back to the upper Eocene.

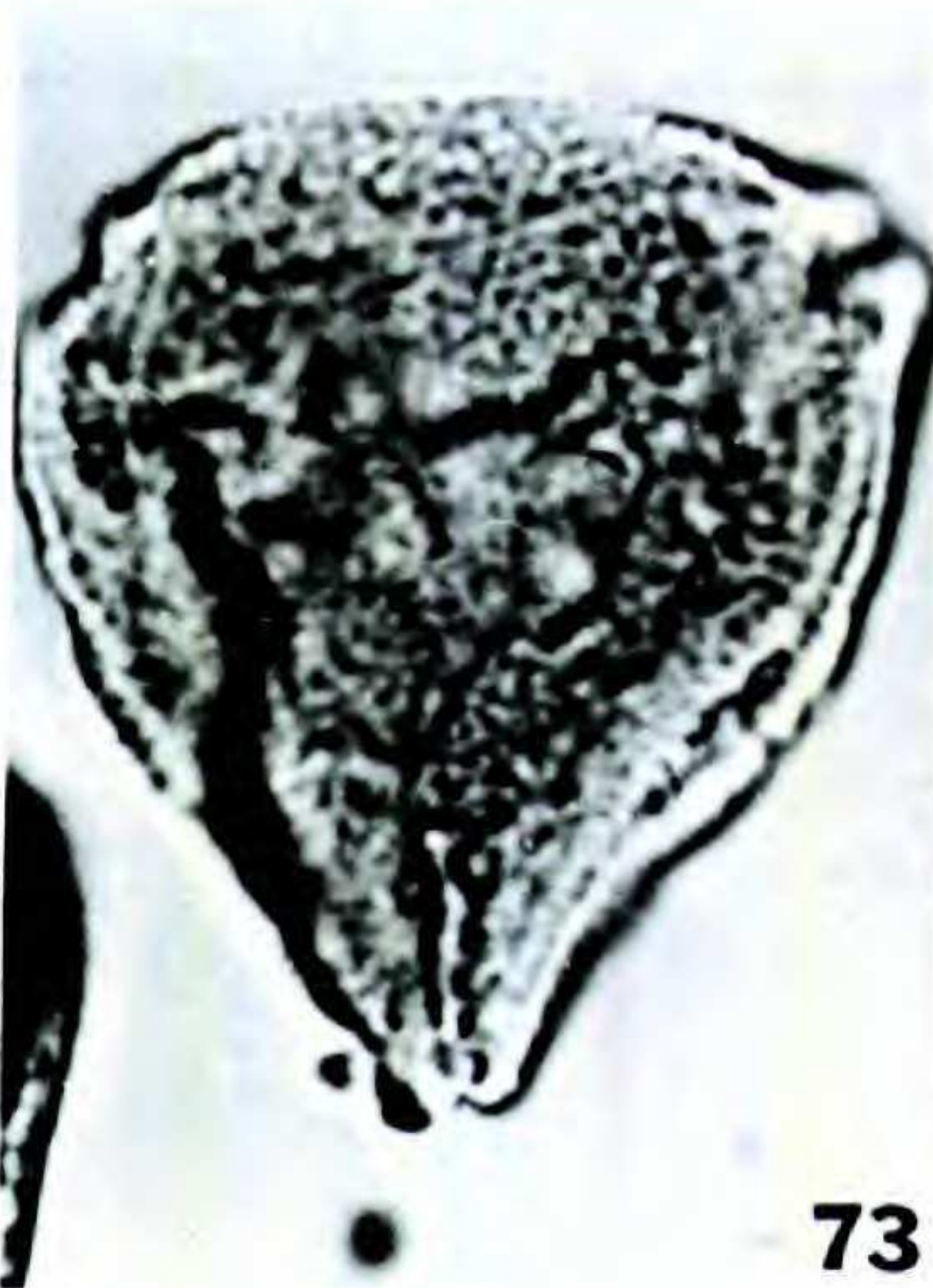
*Serjania* (Figs. 73, 74). Oblate, amb triangular; tricolporate, colpi narrow, straight, 4–6  $\mu\text{m}$  long, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, equidistant, pores slit-like, situated at midpoint

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FIGURES 72–89. 72. *Cardiospermum*, 4-1, D-38,1.—73, 74. *Serjania*, 4-1, S-22,1.—75, 76. *Mortoniiodendron*, 4-1, F-36,3-4; 2-1, M-39,2.—77, 78, 80. *Pelliceria*, 4-1, T-37,1; 4-1, S-27,1.—79. cf. *Chrysophyllum*, 4-1, S-19,2.—81. Unknown 3, 4-1, K-25,2.—82, 83. Unknown 5, 4-1, P-22,4.—84. Unknown 1, 4-1, X-9,2-4.—85. Unknown 2, 4-1, C-19,3.—86, 87. Unknown 7, 9-1, X-35.—88. Unknown 4, 2-1, M-28,4.—89. Unknown 6, 9-1, K-43,1.



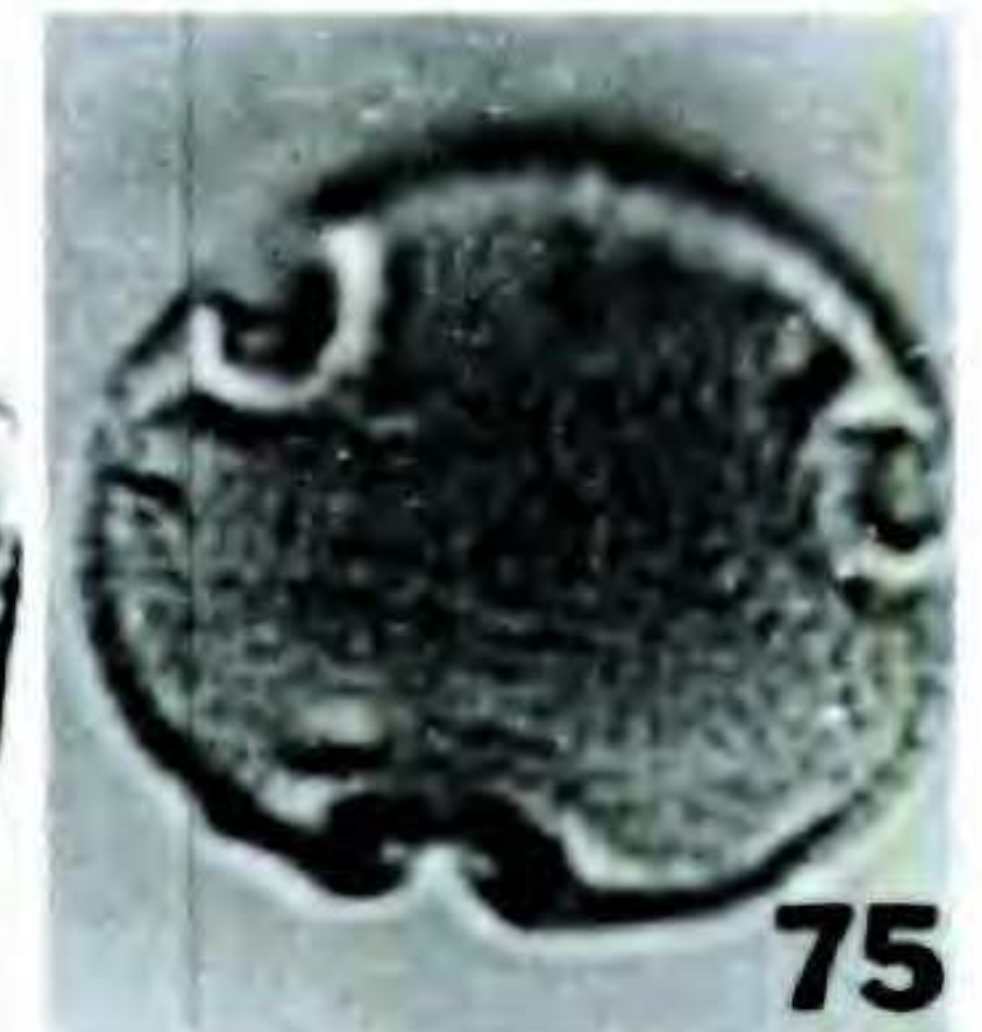
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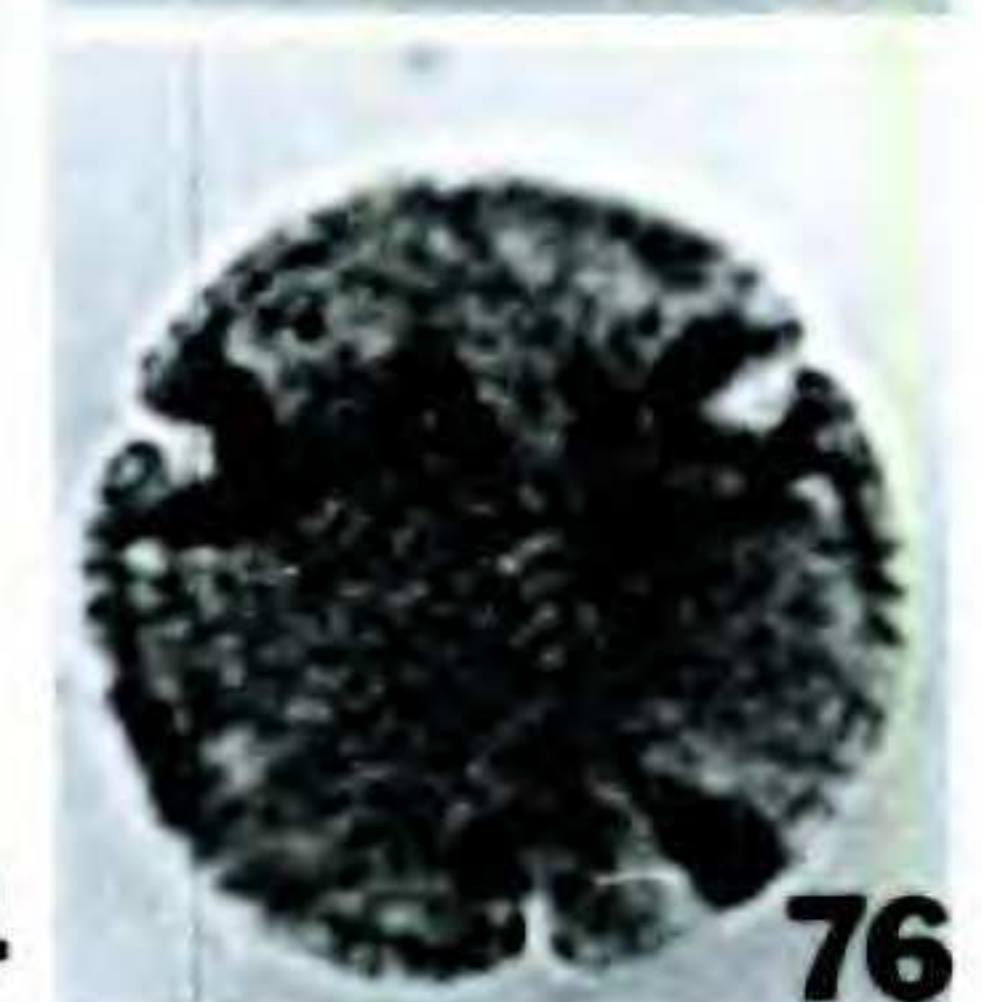
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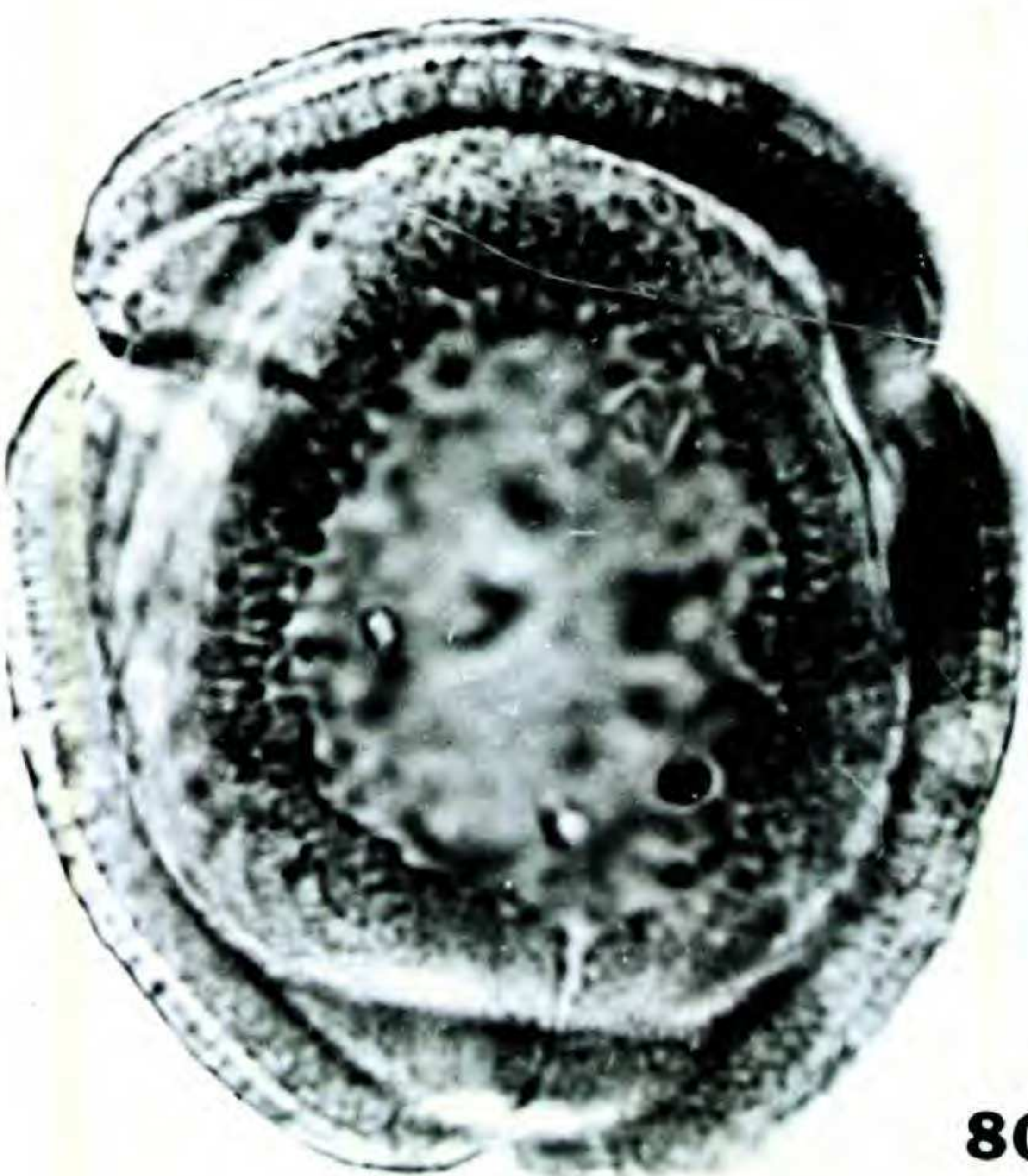
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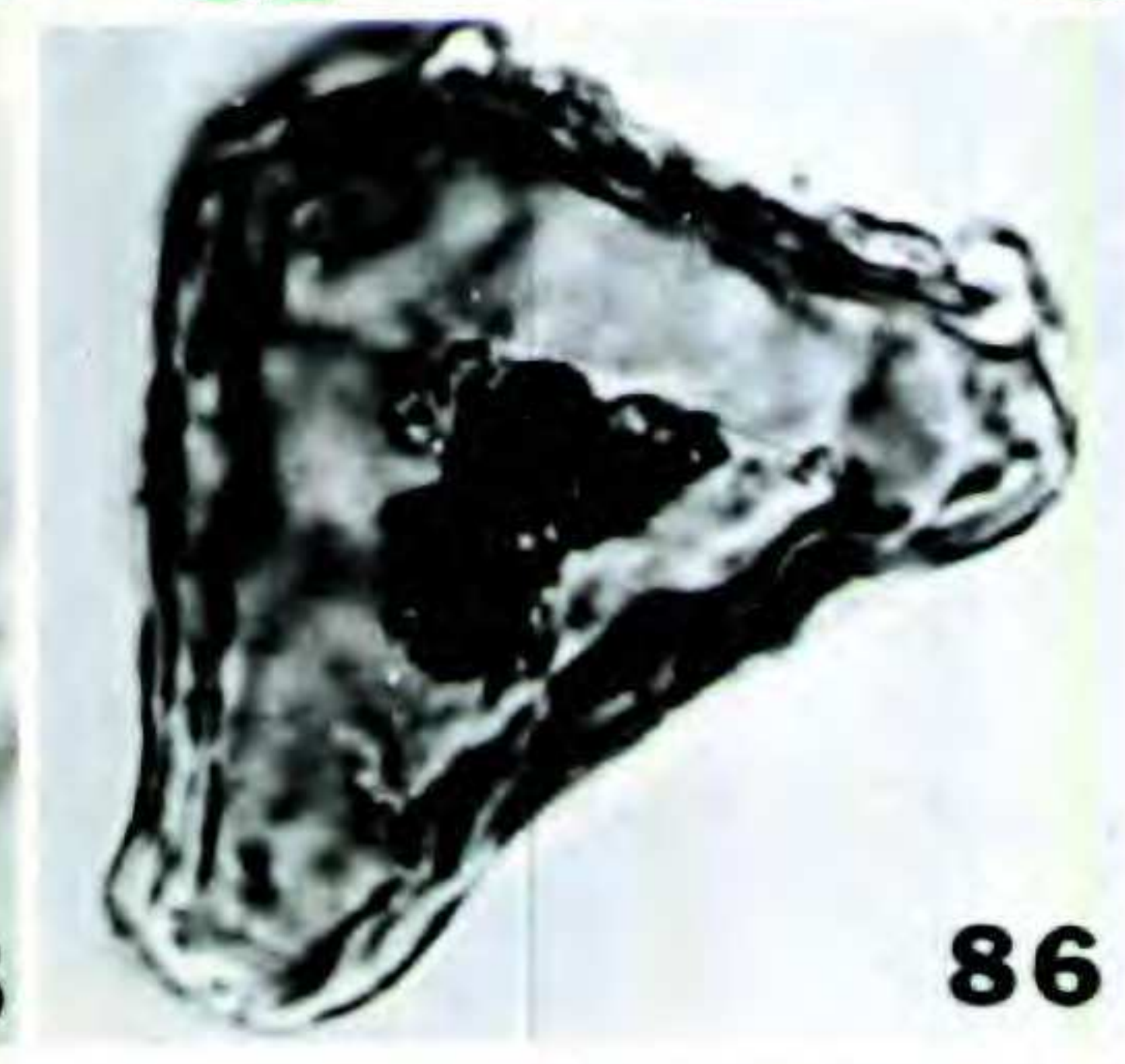
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84



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86



88



89



87

of colpus; tectate-perforate, wall ca. 2  $\mu\text{m}$  thick; finely reticulate; 45  $\mu\text{m}$ .

This genus consists of about 215 species distributed from southern United States to tropical South America. The plants are scandent shrubs or lianas and occur in a wide variety of habitats. Fifteen species are listed for Panama (Croat, 1976). Pollen of *Serjania* is known from the upper Miocene of Veracruz, Mexico (Graham, 1976) and from the Quaternary of Panama (Bartlett & Barghoorn, 1973). The Gatuncillo occurrence extends the range of the genus back to the upper Eocene. Among modern species, the microfossils are similar to *S. conigera* Turcz. of the tropical moist forest.

#### SAPOTACEAE

cf. *Chrysophyllum* (Fig. 79). Prolate, tricolporate, colpi long (25–27  $\mu\text{m}$ ), narrow, straight, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant, costae colpi ca. 1–2  $\mu\text{m}$  wide, pore elongated equatorially (colpi transversalis), ca. 1  $\mu\text{m}$  by 8–10  $\mu\text{m}$ , inner margin entire, situated at midpoint of colpus; tectate, wall 2.5  $\mu\text{m}$  thick; psilate to faintly scabrate; 52–54  $\mu\text{m}$  by 28–32  $\mu\text{m}$ .

*Chrysophyllum* is a large genus of tropical trees (150 species), especially well-represented in the American tropics. The microfossils are similar to several genera of the Sapotaceae (e.g., *Micropholis*, *Pouteria*) but more commonly resemble *Chrysophyllum* in quantitative details; hence, the designation cf. *Chrysophyllum*. There is considerable range in size among the species (18–46  $\mu\text{m}$  in length), and a smaller form (13.5  $\mu\text{m}$  by 18.9  $\mu\text{m}$ ) is reported from the middle Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969). The Gatuncillo specimens are larger (52–54  $\mu\text{m}$ ) and extend the range of this pollen type from the middle Oligocene to the upper Eocene.

#### THEACEAE

*Pelliceria* (Figs. 77, 78, 80). Oblate, amb oval-triangular to nearly circular; tricolporate, colpi narrow, straight, 15  $\mu\text{m}$  (equator to apex) (P.I. 0.4), inner margin entire, equatorially arranged, meridionally elongated, equidistant, colpi transversalis 1  $\mu\text{m}$  by 12–14  $\mu\text{m}$ , situated at midpoint of colpus; tectate to tectate-perforate, wall thick (7–10  $\mu\text{m}$ ), separation of ectexine from endexine clearly evident on most specimens; sculpture variable from mound-like clusters (verrucae) with

subreticulum, to distinctly reticulate; size variable, ca. 50–70  $\mu\text{m}$ .

The pollen morphology and fossil record of *Pelliceria* has been summarized by Graham (1977). Although presently confined to lowland, coastal areas from Costa Rica to northwestern Colombia, the genus is widespread in Caribbean Tertiary deposits. In the stratigraphic literature the specimens are referred to the form-genus *Psilatricolporites crassus* van der Hammen & Wymstra. It is known from the lower middle Eocene of Jamaica, upper Eocene of Panama, middle Oligocene of Puerto Rico (Graham & Jarzen, 1969), Oligo-Miocene of Chiapas, Mexico (Langenheim et al., 1967), and the Tertiary of the Guiana Basin (van der Hammen & Wymstra, 1964). A notable feature of modern *Pelliceria* pollen is the extensive range in size and sculpture patterns, which is also matched by the microfossils. Pollen of *Pelliceria* is common in the Gatuncillo Formation and was probably an important component of the fringing mangrove vegetation.

#### TILIACEAE

*Mortoniendron* (Figs. 75, 76). Peroblate, amb oval-triangular to circular; tricolporate, colpi short (3  $\mu\text{m}$  equator to apex), apices ca. rounded, inner margin entire, equatorially arranged, meridionally elongated, equidistant, conspicuous costae colpi ca. 1.5–2  $\mu\text{m}$  wide; tectate-perforate; finely reticulate, reticulum closed, regular, muri ca. 0.5  $\mu\text{m}$  wide, straight, surface psilate, margins entire; 23–32  $\mu\text{m}$ .

Pollen of *Mortoniendron* and its fossil record has been summarized by Graham (1979b). In that report microfossils had not been recovered from the Gatuncillo Formation, so these specimens represent new occurrences in the Caribbean Tertiary. Other records include the middle Miocene Gatun Formation of Panama (Graham, 1979b), the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976), and the Quaternary of Panama (Bartlett & Barghoorn, 1973). Similar fossils have been reported by Tschudy and van Loenen (1970) under the name *Tiliaepollenites* from the upper Eocene of Mississippi. The complete stratigraphic range, as presently known, is upper Eocene to Recent. There are about five species of these small shrubs to tall trees growing from southern Mexico through Central America. They are most characteristic of tall moist forests. The diversity in

fossil pollen illustrated by Graham (1979b) suggests that other species or related taxa may yet be described from modern tropical forests.

#### UNKNOWNNS

In addition to these specimens, there are others in the Gatuncillo Formation for which biological affinities are unknown. The number of such specimens increases with age of the strata, and the point at which most fossil pollen cannot be referred to a modern genus or family is frequently in a broad transition zone between the upper and middle Eocene. Consequently, the upper Eocene microfloras include a mixture of specimens that can be referred to modern genera or families, depending on the amount of variation in the modern analogs (the 'knowns'); others for which modern representatives simply have not yet been encountered in the reference collection or literature (the unknowns); and a substantial number that are not known to match the pollen of any extant taxa and probably represent extinct forms (the unknowables). The last decrease upward toward the Oligocene and younger strata, and increase below the upper Eocene to the point that they begin to significantly hamper the reconstruction of paleocommunities and paleoenvironments is based on fossil palynomorphs. Reworked palynomorphs, which can be a special problem in lignites, further complicate the assemblage although these can usually be recognized by their corroded appearance, darker color, and/or distinct morphology (especially if redeposited from Paleocene or older sediments).

The most common unknowns from the Gatuncillo Formation are illustrated in Figures 81–144 and briefly described below. These undoubtedly include both extinct forms and those for which biological affinities will ultimately be established in future studies.

#### UNKNOWN ECHINATE TYPES

Type 1 (Fig. 84). Spherical, amb circular; non-aperturate; tectate, wall 1  $\mu\text{m}$  thick; echinate, spines ca. 1  $\mu\text{m}$ , evenly spaced, moderately dense (1.5–2  $\mu\text{m}$  between spines); small (10  $\mu\text{m}$ ).

Type 2 (Fig. 85). Oblate, amb oval-triangular; tricol(poroid?)ate, colpi ca. 3  $\mu\text{m}$  wide at equator, tapering to acute apex, 6–7  $\mu\text{m}$  long (P.I. 0.2), inner margin entire, equatorially arranged, meridionally elongated, equidistant; tectate, wall 1.5  $\mu\text{m}$  thick; echinate, echinae short (2  $\mu\text{m}$ ), acute, some slightly curved, ca. evenly spaced,

moderately dense (ca. 3  $\mu\text{m}$  between spines); 18  $\mu\text{m}$ .

Type 3 (Fig. 81). Spherical, amb circular; non-aperturate (possibly monocolpate?); tectate, wall 1.5–2  $\mu\text{m}$  thick; echinate, echinae short (2  $\mu\text{m}$ ), blunt, ca. evenly spaced, moderately dense (ca. 3  $\mu\text{m}$  between spines); 23  $\mu\text{m}$ .

Type 4 (Fig. 88). Spherical, amb circular; non-aperturate; tectate, wall 1.5  $\mu\text{m}$ ; echinate, echinae short (2–4  $\mu\text{m}$ ), longer ones curved, acute, widely spaced (6–7  $\mu\text{m}$ ); 39  $\mu\text{m}$ .

Type 5 (Figs. 82, 83). Prolate; tricol(poroid?)ate; colpi 18–20  $\mu\text{m}$  long, inner margin entire, equatorially arranged, meridionally elongated, equidistant, possibly slight costae colpi; tectate, wall thick (3–4  $\mu\text{m}$ ), separation of ectexine and endexine clearly evident; minutely echinate; 27  $\mu\text{m}$ .

#### UNKNOWN INTECTATE TYPE

Type 6 (Fig. 89). Spherical, amb circular; non-aperturate; intectate, columellae short, mound-like, slightly elongated baculae, some constricted at base (clavae/gemmae), diam. of sculpturing elements 2–4  $\mu\text{m}$ , smooth, some ca. hyaline, moderately dense (2–4  $\mu\text{m}$  between sculpturing elements); 40  $\mu\text{m}$ .

#### UNKNOWN TRIANGULAR TYPE

Type 7 (Figs. 86, 87). Oblate, amb triangular, outer margin undulating; triporate, pores circular, diam. 4–5  $\mu\text{m}$ , inner margin entire, situated at apices of triangular grain, equidistant; tectate, wall thick (ca. 3  $\mu\text{m}$ ), separation of ectexine and endexine evident; psilate to faintly scabrate, some coarser, irregular sculpturing elements evident in equatorial region near pores; 31  $\mu\text{m}$ .

#### UNKNOWN OBLATE/OBLATE-SPHEROIDAL TYPES

Type 8 (Figs. 90, 91). Oblate-spheroidal, amb ca. circular; tricolpate, colpi 34  $\mu\text{m}$  long (full length), inner margin entire, slight margo formed by diminution of reticulum along colpus margin, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall 2  $\mu\text{m}$  thick; reticulate, reticulum closed, muri thin, smooth, slightly sinuous, diam. of lumen ca. 4  $\mu\text{m}$ ; 36  $\mu\text{m}$ .

Type 9 (Figs. 92–95). Oblate, amb oval-triangular; tricolpate, colpi short, approaching pores, diam. 3–4  $\mu\text{m}$ , equatorially arranged, equidistant; tectate-perforate, wall 1.5  $\mu\text{m}$  thick; retic-

ulate, reticulum closed, regular, muri thin, smooth, diam. of larger lumen ca. 3  $\mu\text{m}$ ; 20–22  $\mu\text{m}$ .

The specimen in Figures 94 and 95 may be a slightly flattened, corroded form of the specimen in Figures 92 and 93. They are representative of rubiaceous types of pollen common in the Gattuncillo Formation.

Type 10 (Figs. 96, 97). Oblate, amb circular; tricolporate, colpi faint, 14–16  $\mu\text{m}$ , equatorially arranged, meridionally elongated, equidistant, pore large (diam. 8–10  $\mu\text{m}$ ), situated at midpoint of colpus; tectate-perforate, wall 2.5  $\mu\text{m}$  thick; reticulate, reticulum closed, ca. regular, muri thin, smooth, diam. of larger lumen ca. 2  $\mu\text{m}$ ; 33  $\mu\text{m}$ .

Type 11 (Figs. 98, 99). Oblate, amb circular; triporate, pores circular, 2.5  $\mu\text{m}$ , narrow annulus, inner margin entire, equatorially arranged, equidistant; tectate, wall 1.5  $\mu\text{m}$  thick; scabrate (possibly microreticulate); 22  $\mu\text{m}$ .

Type 12 (Fig. 100). Oblate, amb circular; tricolpate, colpi 10  $\mu\text{m}$ , extending within 4  $\mu\text{m}$  of pole (P.I. 0.2), tapering to acute apex, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall 1–1.5  $\mu\text{m}$  thick; finely reticulate; 20  $\mu\text{m}$ .

Type 13 (Fig. 101). Oblate, amb circular; tricolporate, colpi 5–6  $\mu\text{m}$ , extending within 5  $\mu\text{m}$  of pole (P.I. 0.2), apex acute, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, pore conspicuous, diam. 3  $\mu\text{m}$ , narrow annulus ca. 1  $\mu\text{m}$ ; tectate-perforate, wall 1.5  $\mu\text{m}$  thick; finely and regularly reticulate; 23  $\mu\text{m}$ .

Type 14 (Fig. 102). Oblate, amb triangular; tricolporate, colpi short (3–4  $\mu\text{m}$ ), narrow (P.I. 0.2), tapering to acute apex, inner margin entire, equatorially arranged, meridionally elongated, equidistant, pore elongated equatorially, 1  $\mu\text{m}$  by 3  $\mu\text{m}$ , situated at midpoint of colpus; tectate, wall 1.5  $\mu\text{m}$  thick; psilate (punctations, possibly artifacts); 13  $\mu\text{m}$ .

Type 15 (Fig. 103). This grain is similar to

Unknown 14 except it is more oval-triangular, the wall is slightly thinner, and the surface appears more sculptured (faintly rugulate, possibly some punctations).

Type 16 (Figs. 104, 105). Oblate-spheroidal, amb circular; tricolporate, colpi long (12  $\mu\text{m}$ ), narrow, inner margin entire, equatorially arranged, meridionally elongated, equidistant, narrow costae colpi, pore elongated equatorially, situated at midpoint of colpus; tectate-perforate, wall 1.5–2  $\mu\text{m}$  thick; reticulate, reticulum closed, regular, diminishing along colpus (faint margo), muri smooth, equal in diam. to lumen (ca. 1  $\mu\text{m}$ ) giving punctate effect, appearing ca. linearly aligned; 18  $\mu\text{m}$ .

Type 17 (Fig. 106). Oblate, amb circular; tricolpate, colpi 12  $\mu\text{m}$ , tapering to acute apex, straight, inner margin ca. entire, extending within 6  $\mu\text{m}$  of pole (P.I. 0.2), equatorially arranged, meridionally elongated, equidistant; intectate, columellae thin needle-like baculae, some slightly clavate; ca. 2  $\mu\text{m}$  long; 30  $\mu\text{m}$ .

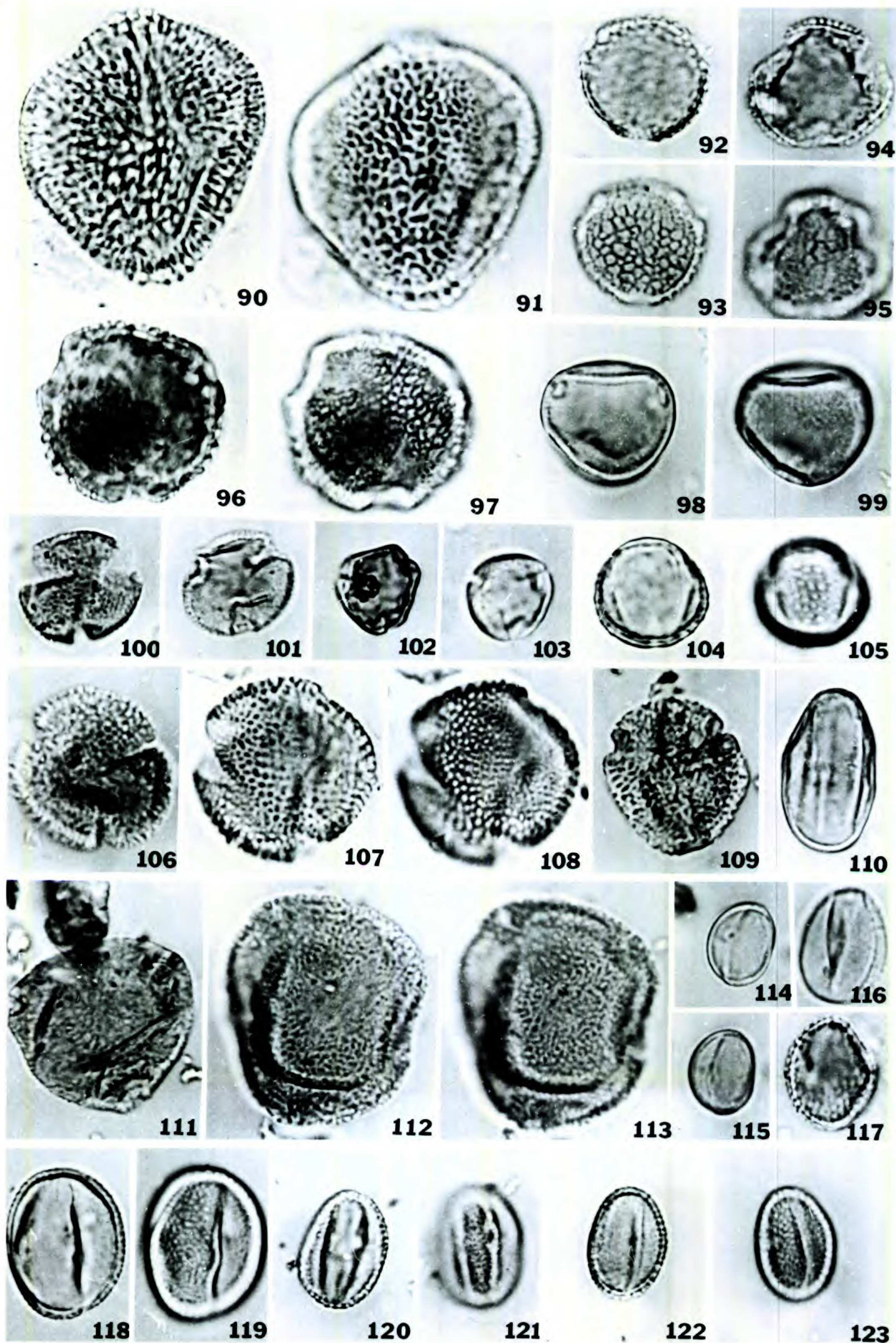
Type 18 (Figs. 107, 108). Oblate, amb circular; tricolpate, colpi 10  $\mu\text{m}$  long, extending within 6  $\mu\text{m}$  of pole (P.I. 0.2), tapering to acute apex, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall thin in relation to diam. of grain (1–1.5  $\mu\text{m}$ ); reticulate, reticulum closed, regular, width of muri and diam. of lumen ca. 1  $\mu\text{m}$ ; 30  $\mu\text{m}$ .

Type 19 (Fig. 109). Oblate, amb circular to oval-triangular; triporate (short colpi), pores slightly elongated meridionally, 1  $\mu\text{m}$  by ca. 3  $\mu\text{m}$ , inner margin entire, conspicuous costae pori (colpi) 2.5  $\mu\text{m}$  wide, pores equatorially arranged, equidistant; tectate-perforate, wall 1.5  $\mu\text{m}$  thick; reticulate, reticulum regular, closed, moderately fine (diam. of lumen 1–2  $\mu\text{m}$ ); 27  $\mu\text{m}$ .

Type 20 (Fig. 111). Oblate, amb oval-triangular; tricolporate, colpi short, faint, equatorially arranged, meridionally elongated, equidistant, pores elongated equatorially (1  $\mu\text{m}$  by 3  $\mu\text{m}$ ), situated at midpoint of colpus, costae pori, slightly

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FIGURES 90–123. 90, 91. Unknown 8, 4-1, W-9,1.—92–95. Unknown 9, 4-1, N-15; 4-1, W-23,1-3.—96, 97. Unknown 10, 9-1, D-35,1.—98, 99. Unknown 11, 4-1, E-30,1.—100. Unknown 12, 4-1, N-10,2-4.—101. Unknown 13, 4-1, S-23,1-3.—102. Unknown 14, 9-1, J-18,3.—103. Unknown 15, 4-1, W-27,2.—104, 105. Unknown 16, 4-1, T-40,2.—106. Unknown 17, 4-1, E-28,1-2.—107, 108. Unknown 18, 4-1, S-8,3.—109. Unknown 19, 2-1, O-24.—110. Unknown 22, 4-1, O-24.—111. Unknown 20, 2-1, T-17,1-3.—112, 113. Unknown 21, 4-1, E-33,2.—114, 115. Unknown 23, 4-1, H-13,2-4.—116. Unknown 24, 4-1, V-34,1-2.—117. Unknown 25, 1-4, N-28,2-4.—118, 119. Unknown 26, 4-1, V-42.—120, 121. Unknown 27, 4-1, Q-27,1.—122, 123. Unknown 28, 4-1, K-31.



aspidate; tectate, wall 1.5  $\mu\text{m}$  thick; rugulate-striate; 32  $\mu\text{m}$ .

Type 21 (Figs. 112, 113). Oblate, amb ca. circular; stephanoporate (short colpi; 5 in number), pores slit-like, equatorially arranged, equidistant; tectate-perforate, wall thin (1.5  $\mu\text{m}$ ); finely reticulate; 40  $\mu\text{m}$ .

#### UNKNOWN PROLATE, TRICOL(POR)ATE TYPES

Type 22 (Fig. 110). Prolate; tricolpate, colpi long (24  $\mu\text{m}$ ), narrow, straight, apices acute, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate, wall 1.5  $\mu\text{m}$  thick; psilate to faintly scabrate; 27  $\mu\text{m}$  by 15  $\mu\text{m}$ .

Type 23 (Figs. 114, 115). Prolate; tricolporate, colpi long (12  $\mu\text{m}$ ), narrow, straight, apices acute, inner margin entire, equatorially arranged, meridionally elongated, equidistant, pores faint, situated at midpoint of colpus; tectate, wall 1  $\mu\text{m}$  thick; psilate to faintly scabrate; 15  $\mu\text{m}$  by 12  $\mu\text{m}$ .

Type 24 (Fig. 116). Prolate; tricolpate, colpi long (16  $\mu\text{m}$ ), narrow, straight, apices acute, inner margin entire, equatorially arranged, meridionally elongated, equidistant; tectate, wall 1  $\mu\text{m}$  thick; faintly scabrate; 20  $\mu\text{m}$  by 14  $\mu\text{m}$ .

Type 25 (Fig. 117). Prolate; tricolporoidate, colpi long (16  $\mu\text{m}$ ), narrow, straight, inner margin entire, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, reticulate, diam. of lumen ca. 1  $\mu\text{m}$ ; 20  $\mu\text{m}$  by 18  $\mu\text{m}$ .

Type 26 (Figs. 118, 119). Prolate; tricolpate, colpi long (24  $\mu\text{m}$ ), narrow, straight, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall 2  $\mu\text{m}$  thick; finely reticulate, diam. of lumen and width of muri ca. 1  $\mu\text{m}$ ; 27  $\mu\text{m}$  by 23  $\mu\text{m}$ .

Type 27 (Figs. 120, 121). Prolate; tricolporate, colpi long (18  $\mu\text{m}$ ), narrow, straight, inner margin entire to minutely dentate, costae colpi 2  $\mu\text{m}$  wide, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall 2  $\mu\text{m}$  thick; finely reticulate, diam. of lumen and width of muri ca. 1  $\mu\text{m}$ ; 27  $\mu\text{m}$  by 23  $\mu\text{m}$ .

Type 28 (Figs. 122, 123). This type is similar to Unknown 27, except costae colpi are not evident.

Type 29 (Figs. 124, 125). Prolate; tricolporate, colpi long (18  $\mu\text{m}$ ), narrow, straight, inner margin entire to minutely dentate, costae colpi 2.5  $\mu\text{m}$  wide, equatorially arranged, meridionally elongated, equidistant, pore circular, 2  $\mu\text{m}$ , inner margin entire, situated at midpoint of colpus; tectate-perforate, wall 1.5  $\mu\text{m}$  thick; finely reticulate, reticulum closed, regular, diam. of lumen and width of muri ca. 1  $\mu\text{m}$ ; 21  $\mu\text{m}$  by 18  $\mu\text{m}$ .

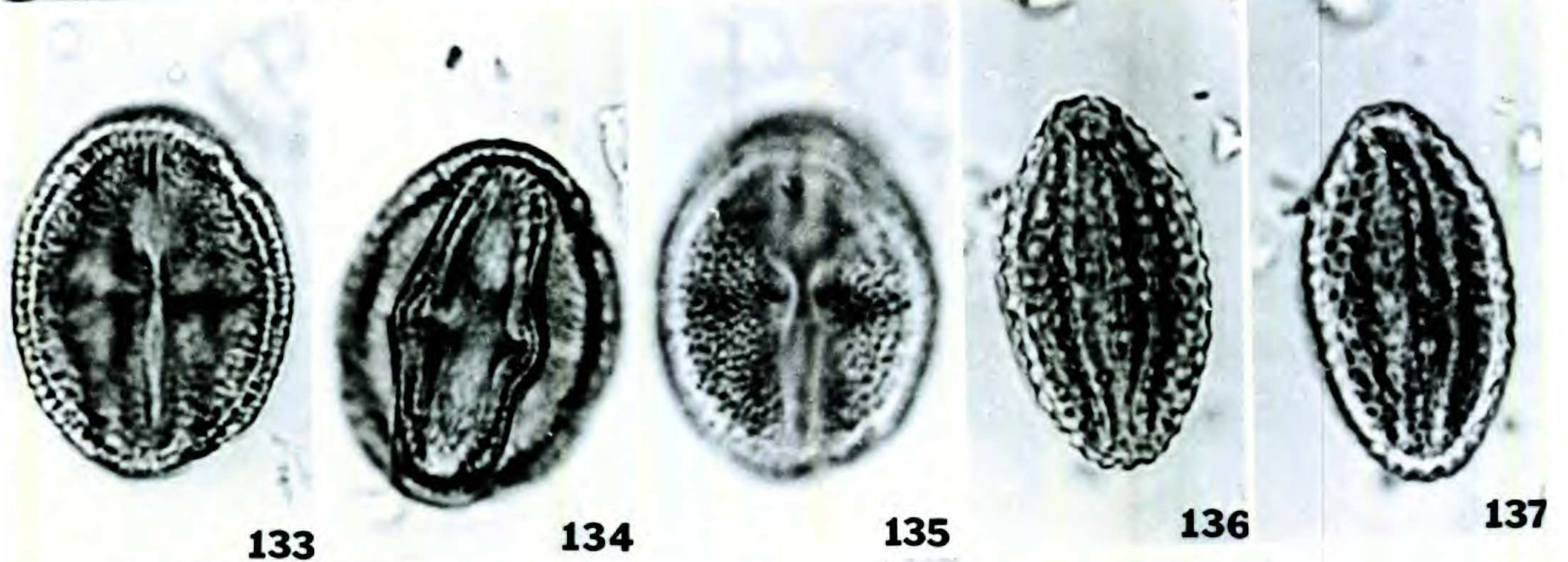
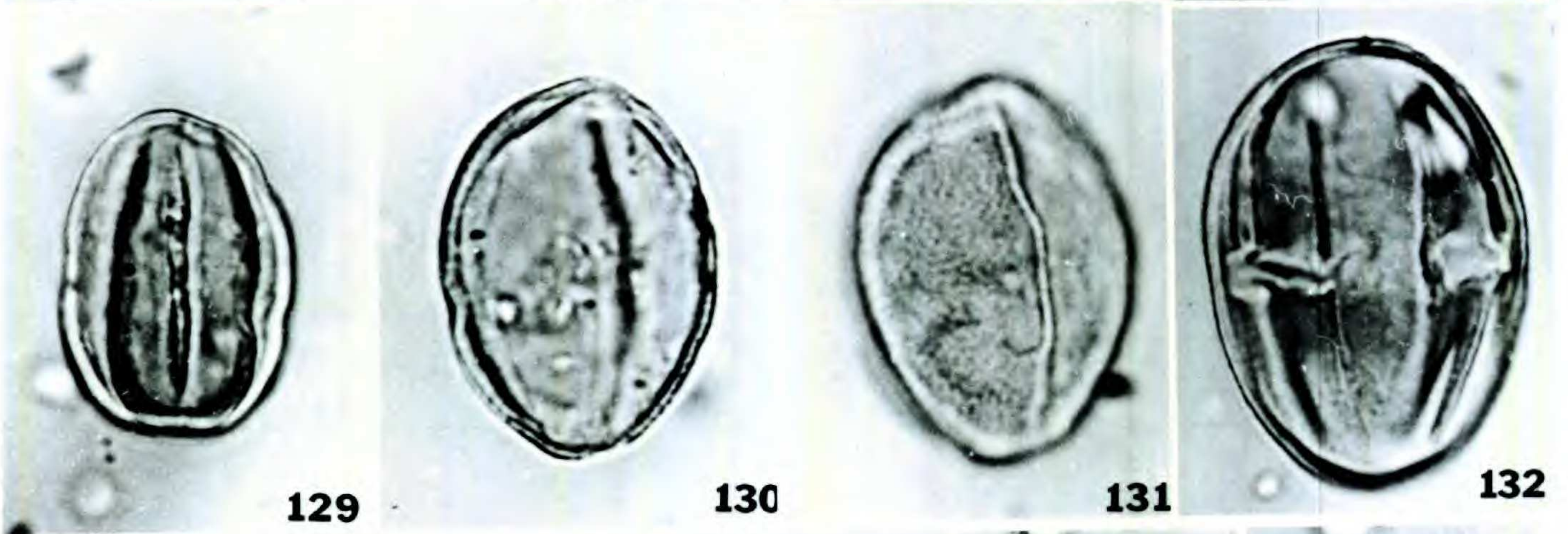
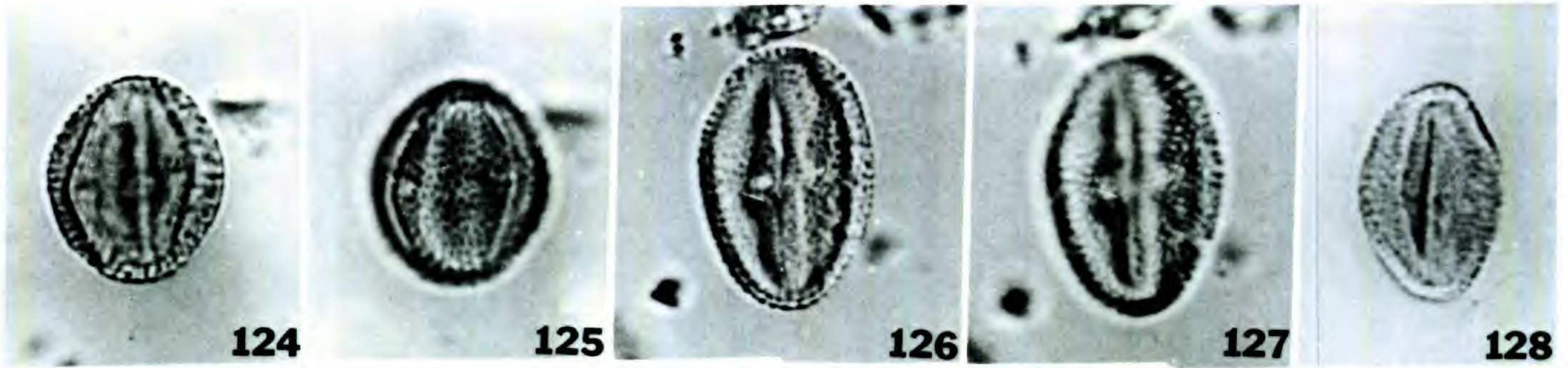
Type 30 (Figs. 126, 127). Prolate; tricolporate, colpi long (22  $\mu\text{m}$ ), narrow, straight, inner margin entire to minutely dentate, costae colpi 3  $\mu\text{m}$  wide, equatorially arranged, meridionally elongated, equidistant, pore slightly elongated equatorially (1.5  $\mu\text{m}$  by 3  $\mu\text{m}$ ), situated at midpoint of colpus; tectate-perforate, wall 1.5  $\mu\text{m}$  thick; finely reticulate, reticulum closed, regular, diam. of lumen and width of muri ca. 1  $\mu\text{m}$ ; 27  $\mu\text{m}$  by 19  $\mu\text{m}$ .

Type 31 (Fig. 128). This specimen is similar to Unknown 30, but slightly smaller (22  $\mu\text{m}$  by 14  $\mu\text{m}$ ).

Type 32 (Fig. 129). Prolate; tricolpate, colpi long (28  $\mu\text{m}$ ), narrow, straight, inner margin minutely dentate, apices acute, membrane sparsely granular, equatorially arranged, meridionally elongated, equidistant; tectate, wall 1.5–2  $\mu\text{m}$  thick; psilate to faintly striate; 33  $\mu\text{m}$  by 23  $\mu\text{m}$ .

Type 33 (Figs. 130, 131). Prolate; tricolpate, colpi long (32  $\mu\text{m}$ ), narrow, straight to slightly sinuous, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate to minutely tectate-perforate, wall 1.5  $\mu\text{m}$  (thin in relation to size of grain); very finely reticulate; 36  $\mu\text{m}$  by 27  $\mu\text{m}$ .

Type 34 (Fig. 132). Prolate to prolate-spheroidal; tri(to possibly tetra-)colporate, colpi long (38–40  $\mu\text{m}$ ), narrow, straight, apices acute, costae colpi ca. 3  $\mu\text{m}$  wide, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant, pores conspicuous, oval (13  $\mu\text{m}$  by 5  $\mu\text{m}$ ), inner margin entire, situated at midpoint of colpus; tectate, wall 1.5–2  $\mu\text{m}$  thick; minutely reticulate; 45  $\mu\text{m}$  by 33  $\mu\text{m}$ .





Type 35 (Figs. 133–135). Prolate to prolate-spheroidal; tricolporate, colpi long (30  $\mu\text{m}$ ), narrow, straight, inner margin entire, apices acute, costae colpi 4  $\mu\text{m}$  wide, pores (endoapertures) elongated equatorially (2–2.5  $\mu\text{m}$  by 4–4.5  $\mu\text{m}$ ), situated at midpoint of colpus; tectate-perforate, wall 2.5–3  $\mu\text{m}$  thick, ectexine clearly distinct from endexine; finely reticulate, diam. of lumen ca. 1  $\mu\text{m}$ ; 36  $\mu\text{m}$  by 29  $\mu\text{m}$ .

Type 36 (Figs. 138, 139). This species is similar to Unknown 35, but is slightly larger (41  $\mu\text{m}$  by 24  $\mu\text{m}$ ) with a thinner exine (1.5–2  $\mu\text{m}$ ). Both are similar to several members of the Anacardiaceae but also overlap in morphology with some Euphorbiaceae.

Type 37 (Figs. 136, 137). This specimen (40  $\mu\text{m}$  by 21  $\mu\text{m}$ ) is typical of the prolate, tricolporate, costate, reticulate type previously described, but is distinctive in that the sharp edges of the muri give a characteristic ‘scooped out’ appearance to the exine.

Type 38 (Figs. 140, 141). This large specimen (68  $\mu\text{m}$  by 40  $\mu\text{m}$ ) is similar to the smaller specimens described as Unknowns 35 and 36, and resembles some Euphorbiaceae, as well as the larger Anacardiaceae. In many specimens of this type, the bases of the columellae are arranged into a subreticulum, and the wall is comparatively thick (3–3.5  $\mu\text{m}$ ).

Type 39 (Fig. 142). This specimen (58  $\mu\text{m}$  by 40  $\mu\text{m}$ ) is also anacardiaceous/euphorbiaceous in aspect but has finer, more delicate columellae and a relatively thin wall (2  $\mu\text{m}$ ).

Type 40 (Figs. 143, 144). This specimen (68  $\mu\text{m}$  by 45  $\mu\text{m}$ ) is of the same general type described for the Anacardiaceae/Euphorbiaceae forms but has a wall intermediate in thickness (2–3  $\mu\text{m}$ ) between Unknowns 38 and 39. Although these minute differences in wall thickness and columellae coarseness are difficult to quantify with exact measurements under light microscopy, such differences do impart recognizable differences between the specimens.

#### PALEOCOMMUNITIES

Arrangement of taxa from the Eocene Gatuncillo Formation into paleocommunities is difficult because of the age of the deposits. The microfossils represent remnants of a vegetation existing ca. 40 Ma, which was a transitional period when many lineages were differentiating into modern taxa (see previous discussion under *Tillandsia*). Consequently, the morphology of nu-

merous specimens do not match, exactly, any modern analog, even though they may clearly be recognized as belonging to a given family. Such specimens often combine the pollen characters of two or more genera that are now palynologically distinct. This is no different in kind from similar problems encountered in younger Tertiary palynofloras; the examples just become more numerous with increasingly older deposits.

Further, it can not always be assumed that the ecological requirements of the fossil representative and its presumed modern analog are identical. This problem is lessened to some degree when paleocommunity reconstructions are based on a large number of genera, rather than on a few genera regarded as key or indicator components. The many unknowns in the Gatuncillo palynoflora also complicate interpretations.

These limitations, however, do not automatically preclude detecting the general kinds of paleocommunities present, even in late Eocene deposits. When fossil taxa cluster into community types that include many genera, based on the habitat of presumed modern analogs, it is likely that assemblage was present, even though individual components may be difficult to identify or may have changed associations through time.

Another problem involved in recognizing paleocommunities based on fossil palynomorphs is a bias toward lowland vegetation and wind-pollinated components. In tropical environments these limitations are minimized, although not eliminated, by the considerable outwashing of pollen into lowland basins of deposition by high rainfall (Germeraad et al., 1968). Muller (1959) demonstrated that pollen from upland communities is readily transported into coastal environments by tropical rivers. For example, the paleocommunities represented in the lignites of the Paraje Solo Formation of Veracruz, Mexico (Graham, 1976) include lowland communities of *Rhizophora* (manglar), the mid-altitude bosque caducifolio, the higher altitude bosque de pino y encino, and the high altitude bosque de oyamel (*Abies*). Although there is some evidence that cooler temperatures shifted the vegetation zones downward (viz., the presence of *Picea* pollen in the sediments), many of these communities were still altitudinally removed some distance from the coastal basin of deposition.

Similarly, the presence of such large, entomophilous pollen types as *Hauya* (Onagraceae, 85  $\mu\text{m}$ ), *Ludwigia* (Onagraceae, 104  $\mu\text{m}$ ), and *Hampea/Hibiscus* (Malvaceae, 135  $\mu\text{m}$ ) in trop-

TABLE 2. Distribution of taxa identified from the middle(?) to upper Eocene Gatuncillo Formation among comparable modern community types in Panama.

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Tropical Moist Forest (21 genera + 1 widespread)

*Selaginella, Ceratopteris, Pteris, Tillandsia, Campnosperma, Casearia, Chrysophyllum, Coccoloba,<sup>b</sup> Combretum, Eugenia,<sup>c</sup> Faramaea,<sup>d</sup> Ficus, Myrcia, Paragonia, Paullinia, Pelliceria, Protium, Rhizophora, Serjania,<sup>a</sup> Terminalia, Tetragastris, Tontalea*

Tropical Wet Forest (19 genera)

*Selaginella, Pteris, Tillandsia, Casearia, Chrysophyllum, Coccoloba, Combretum, Crudia,<sup>e</sup> Eugenia, Faramaea, Ficus, Lisianthus,<sup>f</sup> Mortoniodendron, Myrcia, Paragonia, Paullinia, Protium, Terminalia, Tetragastris*

Premontane Wet Forest (14 genera + 1 widespread)

*Selaginella, Pteris, Tillandsia, Casearia, Coccoloba, Combretum, Eugenia, Faramaea, Ficus, Paragonia, Paullinia, Protium, Serjania<sup>a</sup>, Terminalia, Tetragastris*

Premontane Moist Forest (3 genera + 6 widespread)

*Combretum, Eugenia,<sup>a</sup> Faramaea,<sup>a</sup> Ficus,<sup>a</sup> Ilex, Paullinia,<sup>a</sup> Serjania, Terminalia,<sup>a</sup> Tetragastris<sup>a</sup>*

Premontane Rain Forest (4 genera)

*Casearia, Paullinia, Serjania, Tillandsia*

Tropical Dry Forest (4 genera + 2 widespread)

*Cardiospermum, Casearia, Coccoloba,<sup>a</sup> Combretum, Serjania, Tetragastris<sup>a</sup>*

Premontane Dry Forest (4 genera + 1 widespread)

*Cardiospermum, Casearia,<sup>a</sup> Combretum, Eugenia, Ficus*

Lower Montane Moist Forest (3 genera)

*Pteris, Alfaroa, Engelhardia (Oreomunnea)*

Lower Montane Wet Forest (2 genera)

*Pteris, Tillandsia*

Lower Montane Rain Forest (none)

Montane Wet Forest (none)

Montane Rain Forest (none)

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<sup>a</sup> The genus occurs in this community but is more common or typical in other habitats.

<sup>b</sup> Most common in more or less stressed environments (swamps, beaches, limestone outcrops) but occurs in all lowland life zones.

<sup>c</sup> Myrtales tend to be more common in Panama in more or less stressed environments (e.g., Cerro Jefe) in somewhat drier forest types.

<sup>d</sup> The genus is most common in the tropical wet forest, but the most common species (*F. occidentalis*) is very abundant in the tropical moist forest.

<sup>e</sup> Most common in South America in inundated forests.

<sup>f</sup> Tropical wet forest, but the most common species (*L. skinneri*) is more or less weedy and occurs in drier forest types.

ical sediments (Graham, 1976; Graham & Jarzen, 1969) is witness to the effectiveness of outwashing and water transport in depositing a variety of pollen types in lowland habitats. There are obvious exceptions, such as low pollen-producing communities removed great distances from the basins of deposition (e.g., paramo), or distinctly desert communities where pollen has little chance of long-distance water transport or surviving oxidation under the arid conditions. Evidence for both vegetation types is meager in the Tertiary plant microfossil record for Latin America, but no rational interpretation of the

data would automatically preclude the presence of these communities solely on the basis of the pollen record. It is becoming increasingly apparent, however, that pollen representing lowland, mid-altitude, and even high-altitude communities, including both entomophilous and anemophilous components, and wet to drier ecotypes, are commonly incorporated into lowland basins of deposition in tropical regions. Conversely, when the common and defining elements of a particular community or ecotype are consistently rare or absent in a large tropical Tertiary palynoflora, with such exceptions as noted ear-



FIGURES 142–144. 142. Unknown 39, 4-1, X-8,2-4.—143, 144. Unknown 40, 4-1, X-32,2.

lier, it is likely that assemblage was absent, poorly defined, or restricted in distribution (i.e., not a prominent component of the vegetation).

The taxa represented in the Gatuncillo Formation are arranged according to communities based on the distribution of their presumed modern counterparts (Table 2). The life-zone classification is from Holdridge (1967; Holdridge et al., 1971) and was used by Croat (1978) for describing the vegetation of Barro Colorado Island.

It is noted that the purpose of Table 2 is not to record the complete range of the genera among present-day communities in Central America. Rather, the genera are placed according to their principal or common occurrence in recognition that some are more widely distributed or may contain a species that extends beyond the range typical for the rest of the genus. Some examples are indicated by the designation (1) and by the footnotes in Table 2. In instances in which a fossil pollen type is similar to two genera (*Eugenia/Myrcia*, *Combretum/Terminalia*; Graham, 1980), both are listed to maximize the number of communities potentially represented in the Gatuncillo palynoflora.

When these genera are assigned to life-zones, using distributions cited by Croat (1978), family treatments in the "Flora of Panama," and comments provided by Croat and Gentry (pers. comm.), an obvious pattern emerges (Table 2). Elements from lowland, moist communities constitute the overwhelming majority in the Gatun-

cillo assemblage. Equally evident is the abrupt decrease in genera characteristic of 1) montane, and 2) dry forest types. Even within the constraints on interpretation previously discussed, and acknowledging that some genera range beyond the communities listed in Table 2, it is difficult to avoid the conclusion that higher altitude and drier vegetation types were poorly represented. A conservative interpretation of the existing data is that the listings in Table 2 probably reflect, in a general way, the relative importance of the paleocommunities characterizing the late Eocene landscape in this part of central Panama. The principal paleocommunities present were the tropical moist forest, tropical wet forest, and premontane wet forest. Less prominent were the premontane moist forest, premontane rain forest, tropical dry forest, and premontane dry forest, although representation in these forest types is so low, and involves primarily genera that are also found elsewhere, that some may have been poorly developed or absent. In the lower montane moist forest it is noted that *Alfaroa* and *Engelhardia* (*Oreomunnea*) are both included because the pollen cannot consistently be distinguished under the magnifications of light microscopy, and the specimens are rare in the assemblage (Table 1; ca. three specimens recovered). This forest type, together with the lower montane wet forest, lower montane rain forest, montane wet forest, and montane rain forest were probably poorly represented or absent in the re-

gion. This general reconstruction of the paleocommunities is consistent with other independent geological and paleontological evidence on paleoenvironments and paleophysiography.

#### PALEOENVIRONMENTS

Reconstruction of paleoenvironments for the Gatuncillo flora is facilitated by information available on the geology (particularly sediment types), marine invertebrate and terrestrial mammal paleontology, and plate tectonic history of the Canal region. These data establish geological and biological parameters within which the paleobotanical results can be interpreted.

The microfossils were recovered from lignite deposits that are common in Tertiary formations throughout the Gulf/Caribbean region. The northernmost limit for any significant present-day lignite deposition in North America is southern peninsula Florida (Cohen & Spackman, 1972; Scholl, 1964a, 1964b). Thus the presence of the lignite itself suggests tropical to subtropical environments. Since these lignites commonly contain pollen of *Rhizophora*, *Conocarpus*, *Avicennia*, *Laguncularia*, and *Pelliceria*, this is further confirmation that the sediments reflect tropical paleoclimates. Finally, the Gatuncillo lignites are associated with coralline limestones characteristic of deposition in near-shore, tropical habitats.

Plate tectonic reconstructions show that during most of the Tertiary the present region of Panama was occupied by a series of volcanic islands located above the subduction zone between the east Pacific (Cocos) and developing Caribbean plates (Coney, 1982; Dengo, 1973). Intense tectonic activity is reflected by more than 113 faults observed within a 3 km section of the Gaillard Cut portion of the Canal (R. H. Stewart, pers. comm.). Volcanic activity is evidenced by widespread basalts, volcanic shales, and tuffs (water-lain volcanic ash) throughout the Tertiary formations of Panama (Stewart et al., 1980). A wealth of biogeographic information is consistent with a model of discontinuous land surface between North and South America during most of the Tertiary, culminating with uplift of the Panama land bridge in latest Pliocene and Pleistocene times (Graham, 1973b; Marshall et al., 1976, 1981, 1982; Raven & Axelrod, 1974; Webb, 1976; Whitmore & Stewart, 1965; Woodring, 1966). This documentation of the insular nature of the landscape is important in interpreting cli-

matic histories because biotas of small- to moderate-sized islands are often more insulated from climatic changes than comparable biotas of inland continental areas. If these islands are of relatively low relief, climatic changes that are well-documented in paleofloras derived from continental areas of more diverse physiography (viz., like those from Veracruz, Mexico or the Andean region) may not be as evident in paleofloras derived from low-lying insular vegetation.

The palynological evidence previously discussed suggests that the Eocene landscape, in the vicinity of the Gatuncillo depositional basin, was of moderately low relief. There is no evidence for either locally deposited or long-distance wind or water transported pollen from montane communities. Equally rare is pollen from dry vegetation types.

Thus, the local paleoenvironmental setting for these late Eocene biotas appears to include a series of volcanic islands of moderate to low relief, bordered seaward by shallow limestone-depositing coralline communities, fringed by mangrove vegetation of *Rhizophora* and *Pelliceria*, supporting inland communities of tropical moist, tropical wet, and premontane wet forests, growing under the general tropical conditions of high and evenly distributed rainfall and high uniform temperatures.

These general paleoclimatic conditions under which the Gatuncillo flora existed can be refined, to some extent, by a comparison with modern communities of similar composition. Normally, communities as old as the late Eocene resemble modern assemblages of comparable habitats only in a very general way. In the case of the Gatuncillo flora, however, there is a modern analog in which virtually all the components of the paleocommunity presently grow together. Gentry (pers. comm.) noted that the fossil palynoflora shows a remarkable resemblance to the lowland, swampy, and bordering vegetation between the Atlantic side of Gatun Lake and Piña, province of Colon. This is an interesting observation since the rainfall at nearby Colon, on the Atlantic side where the vegetation shows considerable similarity to the paleocommunities, is nearly double that at Balboa, on the Pacific side where the vegetation shows distinctly less similarity to the paleocommunities (107.3" versus 68"; Croat, 1978: 3). A very general estimate of temperature regimes is provided by data from the forest floor (versus open clearings) on Barro Colorado Island in Gatun Lake (Rubinoff, 1974, cited in Croat,

1978). There the mean maximum forest floor temperature is 28.0°C and the mean minimum is 21.1°C. Although these figures provide only the most general of estimates for upper Eocene conditions in the vicinity of the Gatuncillo depositional basin, they are of interest as the first approximation of terrestrial paleoenvironments available for all of northern Latin America based on paleobotanical data. As noted earlier, the nearest Eocene floras are in South America, which during this time was isolated between Africa and North America and the Mississippi Embayment floras to the north. More precise reconstructions of regional paleoenvironments must await discovery of other fossil floras from the upper Eocene elsewhere in Central America.

Of biogeographic interest is the list of families provided by Raven and Axelrod (1974) considered to be 1) of South American origin and migrating to North America in Eocene or later times, and 2) those probably already established in North America by the late Eocene. An exact correlation would not be expected because the paleoflora is of an age and location that could preserve the earliest migrants from both continents. Nonetheless it is worthwhile to record the analyses because eventually similar information from other paleofloras, combined with biogeographic studies of the modern vegetation, will allow more precise estimates as to the region of origin of certain angiosperm families. Among the families listed by Raven and Axelrod (1974) as primarily of South American origin and migrating into North America during Eocene or later times, only four are recorded in the Gatuncillo palynoflora: Bromeliaceae, Combretaceae, Flacourtiaceae, and Malpighiaceae. Among those listed as already established in North America by the Eocene, 12 were represented in the Gatuncillo palynoflora: Anacardiaceae, Aquifoliaceae, Araliaceae, Bignoniaceae, Leguminosae (Caesalpinioideae), Moraceae, Myrtaceae, Rubiaceae, Sapindaceae, Sapotaceae, Theaceae, and Tiliaceae. At the family level the palynoflora seems to have somewhat greater affinities with North American-derived elements than with South American ones. None of the families listed by Raven and Axelrod (1974) as primarily characteristic of arid habitats in tropical America were represented in the Gatuncillo assemblage.

Genera identified from the Gatuncillo Formation that have not previously been reported in the fossil record include *Lisianthus* (Gentianaceae) and *Cardiospermum* (Sapindaceae).

Three other tentative reports will have to await additional specimens, and possibly SEM/TEM studies, for confirmation. These include cf. *Paragonia/Arrabidaea* (Bignoniaceae), cf. *Tetragastria* (Burseraceae), and cf. *Tontalea* (Hippocra-tiaceae). All are rare in the assemblage (Table 1). Range extensions are recorded for six pollen types in the Caribbean Tertiary (based primarily on previous stratigraphic ranges summarized by Germeraad et al., 1968; Muller, 1981): *Casearia* (from middle Oligocene), cf. *Ficus* (= *Psiladisporites minimus*; diporate Moraceae), *Faramea* (diporate form, first report; triporate known from middle Oligocene), *Paullinia* (from upper Miocene), *Serjania* (from upper Miocene), and cf. *Chrysophyllum* (from middle Oligocene).

The next palynofloras to be treated in this study are from the Culebra, Cucaracha, and La Boca Formations exposed along the Gaillard Cut section of the Panama Canal (Graham et al., 1985). They will reflect the changes in climate, physiography, and vegetation during a 16 Ma period between the late Eocene (ca. 40 Ma) and the early Miocene (ca. 24 Ma; Harland et al., 1982).

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